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THE DEVELOPMENT OF INFANT -
CAREGIVER RELATIONSHIPS IN
THE COMMON MARMOSET
(Callithrix jacchus)

Janet Locke-Haydon
B.Sc.

Thesis submitted for the degree of Doctor of Philosophy

The Open University

Department of Biology

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The bird and beast their common charge attend
The mothers nurse it, and the sires defend
The young dismissed, to wander earth and air,
There stops the instinct, and there ends the care.
A longer care man's helpless kind demands,
That longer care contracts more lasting bands.

Alexander Pope, 1735



ABSTRACT

The thesis describes a study of infant social development carried out on captive common marmosets (Callithrix jacchus) over the first five months of life while maintained in family groups.

From observations of nine infants from 2 to 22 weeks of age, a detailed quantitative account of the relationships between infants and their caregivers (other family members) has been produced. The amount of time infants spend in different activities with different caregivers varies with the age of the infant and with which caregiver is concerned as infants develop quantitatively and qualitatively different relationships with each type of caregiver. Independence of infants from caregivers is promoted primarily by the caregivers, infants appearing to seek more care than caregivers are prepared to give. Caregivers do not compensate for differences in each others' caregiving behaviour, nor do they compete for access to infants.

From the results of these observations, the distribution of infants' time and activities among family members is suggested to result from the interaction of two factors: the tendency of an infant at a given age to seek a certain level of care, and the tendencies of family members to offer a certain level of care. This caregiving/care-seeking hypothesis generates several predictions which have been tested by experimentally manipulating the behaviour of particular caregivers using a neuroleptic drug to reduce care offered to and social interactions with infants.

Observations of the experimental second group of eight infants have borne out several of the predictions from the hypothesis: Infants whose caregivers are drugged spend less time in non - care-seeking activities and there are some increases in care-seeking behaviour.

Infants continue to seek care from caregivers in order of preference, and no compensation among caregivers is found.

Results from the second group of infants provide support for the caregiving/care-seeking hypothesis but also indicate other factors which need to be taken into account.

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CHAPTER 1 - Introduction

The main objective of this study was to produce a detailed, quantitative account of the social development of infant common marmosets (Callithrix jacchus). It was intended to repeat and extend previous work in this area, to try to extract some underlying factors controlling infant social development, and to manipulate the behaviour of caregivers experimentally to investigate further infant-caregiver relationships in this species. The study is therefore concerned with the causation of behaviour (though at the social and behavioural level, not the neurophysiological level) rather than with its function. Function is clearly an important issue in the study of social behaviour (see review by Kummer, 1979), and in the case of caregiving to young infants the activities of nursing, carrying, cleaning, grooming, food-sharing, protection from predators and conspecifics, control of independence and socialization all have adaptive value to infants (survival) and to caregivers (reproductive success). Discussion of the functional advantages and disadvantages of infant care by non-parents can be found in Blaffer-Hrdy (1976).

In order to understand development in infancy in social mammals such as primates, it is essential to see and analyse the infant's behaviour in a social context. Physical development and social relations are intimately linked and socialization is the process whereby a newborn individual grows up to become a normal and effective member of its society. This is obviously of enormous importance and a great deal of research has focussed on infant development and social relationships in primates ever since Harlow's discovery that contact and security were more important to rhesus monkey infants than simply being fed (Harlow & Zimmermann, 1959).

Important work concerning primate caregiving behaviour and its influence on the development of the young has been a series of studies by R.A. Hinde and his co-workers on captive groups of rhesus macaques (Macaca mulatta). The result has been a clear definition of questions which can be asked about caregiving behaviour, and the development of techniques for observation and for the evaluation of the role partners in a relationship play in determining the characteristics of that relationship. The early work consisted of detailed observations of the behavioural development of young rhesus monkeys living in small captive social groups (Hinde et al, 1964; Hinde & Spencer-Booth, 1967a; reviewed in Hinde, 1971). Because the infants were being reared by their mothers this led to a concentration on mother-infant relations within the groups, and studies were conducted on differences in behaviour between mother-infant pairs with and without other social companions (Hinde & Spencer-Booth, 1967b), and on mother-infant pairs in which the mothers and infants underwent short periods of separation from each other (Hinde, 1969b; Hinde & Davies, 1972; Hinde & Spencer-Booth, 1971a; Hinde et al, 1966).

In order to measure changes brought about by separation experiences it was necessary to develop techniques for describing relationships quantitatively. These techniques include correlating different measures of mother-infant behaviour, and examining the directions (positive or negative) of changes in the measures over time and between mother-infant pairs (Hinde, 1969a & 1975b; Hinde & Atkinson, 1970; Hinde & White, 1974). This allowed a preliminary teasing apart of the roles mother and infant play in the relationship between them and led to a consideration of individual differences between mother-infant pairs and to the concept of qualities of relationships and how to measure them (Hinde & Simpson, 1975; Hinde & Spencer-Booth, 1970 & 1971b).

Finally, relationships between individual mothers and infants are seen not as discrete and discontinuous, but are linked to other relationships within the group. For example, how restricting a mother is towards her infant (mother-infant relationship) depends on whether or not other social companions are present (mother-adult female relationships) (Hinde & Spencer-Booth, 1967b). All relationships present in a group affect each other and form a 'social nexus' which consists of the total social environment as it affects each animal. The social structure of this nexus is described by the content, quality and patterning of relationships occurring within it, and the relationships are in turn described by the interactions which compose them (Hinde, 1975a & 1976).

In the present study, social relationships are described within the framework of the social nexus, using dyadic interactions as the basic unit for describing social structure, and the methods used are derived from Hinde's techniques of data collection and analysis.

To date, most work on infant development and social relationships has been on species in which the mother is the principal caregiver to the infant (though allomothering may occur, as in langurs) and the social unit is a multi-male, multi-female troop. Examples include yellow baboons, Papio cynocephalus (Altmann, 1980), Indian langurs, Presbytis entellus (Jay, 1963; Dolhinow, 1980), and rhesus monkeys (Hinde's work, described above). It is important to extend this line of research to species with multiple caregivers where infants grow up in a different social system, one which approximates more closely that of man. Multiple caregiving occurs when several members of the social group provide extensive care for the infant, frequently taking over responsibility for the infant from the mother. In primates, this only occurs in a few species and all have a nuclear or extended family

group as their basic social unit. These species include all the members of the family Callitrichidae, i.e. marmosets and tamarins (Pook, 1978; Snyder, 1974), also Goeldi's monkey, Callimico goeldii (Moynihan, 1976), owl monkeys, Aotus trivirgatus (Dixon & Fleming, 1981), titis, Callicebus torquatus and C. moloch (Kinzey et al, 1977; Mason, 1966), siamang, Symphalangus syndactylus (Chivers, 1972 & 1974), and of course in some cultures Homo sapiens.

Although the behavioural gap between human and non-human primates is enormous and conclusions drawn from studies of apes and monkeys should not be applied directly to humans, studies of other primates can nevertheless provide useful insights into the understanding of human behaviour provided generalizations to humans are made with the greatest caution and assessed wherever possible against more direct sources of evidence. For example, the study of non-human primates permits the development of methods which can then be adapted for the human case, such as in the diagnosis and treatment of behavioural disorders or in the description and classification of behaviour. Non-human primates can be used for the study of particular problems, where experiments would be impossible using human subjects for ethical or practical reasons. Practical reasons include length of lifespan, number of subjects available, and provision of adequate controls. Problems such as mother-infant attachment and the effects of separation have been tackled in this way. Studies on other primates can also provide principles or generalizations whose relevance to humans can subsequently be assessed. The relative simplicity of non-human primates as compared with humans can highlight theoretical issues and permit the isolation of principles which might be hidden in the complexity of the human case.

Deprivation of normal socialization experiences in human

children can result in a wide range of personal and social deficiencies and aberrations including affective disorders, limited capacity for sustained and effective social relationships, and psychopathic tendencies (Bowlby, 1951; Mason, 1960; Rutter, 1972 & 1979). It is therefore important to examine socialization and the development of infant-caregiver relationships in other multiple caregiver species which are open to experiment in order to provide a full description of the processes involved. This may then allow the pinpointing of any caregivers with whom, or ages at which, certain relationships are of particular importance to the normal development of the infant.

Only one study has looked at infant social development in a multiple caregiver species in comparable quantitative and qualitative detail to the studies of single principal caregiver old world monkeys mentioned above, that of J.C. Ingram (1975a, 1977 & 1978). Ingram studied parent-infant interactions and the development of the young in captive common marmosets (Callithrix jacchus), further details of which are given below. Marmosets are small, new world primates belonging to the family Callitrichidae in the suborder Platyrrhini. They are about the size of tree squirrels, have thick fur, clawed digits (except for the big toe which has a nail), prehensile hands for clinging to large branches, legs which are considerably longer than the arms, and a non-prehensile tail. They are found in Brazil, living in equatorial rain forest and woodland savannah. They are diurnal and arboreal, moving on the larger branches of the open canopy and also in the shrub layer. Their diet includes insects, small birds, mammals and lizards, eggs, fruit, leaves and tree exudates (Ingram, 1975a; Napier & Napier, 1967; Coimbra-Filho & Mittermeier, 1976).

The classification of marmosets and other Platyrrhini used throughout this study is that found in HersHKovitz (1977), with the

exception of Geoffroy's tamarin which is often known as Saguinus geoffroyi (see studies by Hernández-Camacho & Cooper, 1976, and Moynihan, 1970 & 1976) and is referred to as such here, though HersHKovitz places it as a subspecies of Saguinus oedipus, i.e. Saguinus oedipus geoffroyi. Nomenclature for other primates follows Napier & Napier (1967).

Marmosets are of great interest and importance in studies of applied biology as well as from the point of view of models of family group life. Their small size, low cost and relative availability make them easy to maintain in laboratories. There is less risk of disease in marmosets than in macaques (Kingston, 1969), and in comparison with old world primates, marmosets have a high reproductive rate (about four young per year) and short generation time (less than two years). All these factors make marmosets ideal subjects for laboratory studies with a high turnover requiring large numbers of experimental animals. Marmosets have been used extensively in medical studies including such areas as oncology, immunology, genetics, reproductive physiology, toxicology, infectious diseases and drug studies (see papers in Gengozian & Deinhardt, 1978), and behavioural studies are needed to back up and extend conclusions drawn from experimental work. Behavioural side-effects cannot be detected if the full range of normal behaviours and social relations has not already been described in detail.

Marmosets are also particularly useful for work on social behaviour since a nearer approximation to the group structure occurring under natural conditions can be obtained in the laboratory than is possible with larger species (Stevenson, 1977).

Ingram's study of infant development and social relationships in common marmosets emphasized that the father frequently interacted with his infants, normally carrying them from birth for approximately the same

amount of time per day as the mother. Adults protected their new offspring by an increased frequency of aggressive threat displays towards other monkeys and observers. Adolescent and sub-adult females were attracted by the presence of infants and helped in their care and transport. Amongst siblings, sub-adults (10 - 15 months) were most involved in caring for newborn infants, having gained experience from handling the previous babies. Older siblings interacted with infants more than parents while the infants were not being carried.

Parents were responsible for the maintenance of proximity with infants up to the end of the third week while infant locomotor ability was limited, and both maternal and paternal rejections were highest when the infants were about 10 - 11 weeks old which corresponds to a weaning period. Infants were more involved in maintaining proximity with their mothers than with their fathers, and both parents (particularly the mother) were responsible for promoting and regulating the increase in infant independence. Overall there was co-operation between parents and siblings in the care of the infants.

Other work concentrating on social relations within family groups of Callitrichids, though in less detail than the above study, has been carried out by Box on Callithrix jacchus and Saguinus mystax (Box, 1975a, 1975b, 1977 & 1978; Box & Morris, 1980), by Epplé and by Vogt on S. fuscicollis (Epplé, 1975; Vogt, 1978; Vogt et al, 1978), and by Welker on C. jacchus and S. oedipus (Welker et al, 1981).

Virtually no fieldwork has been carried out on the social behaviour of free-living marmosets, though what has been done tends to support the conclusions of the captive studies. For example, marmosets appear to live in small groups consisting of one adult pair which breed and a variable number of other individuals which, if adult, do not breed, and most of which are probably offspring of the adult pair. This suggests

that the family is the basic social unit. This has been observed for Callithrix jacchus (Stevenson, 1978b), C. humeralifer (Rylands, 1981), Cebuella pygmaea (Castro & Soini, 1977; Izawa, 1976), Leontopithecus rosalia (Coimbra-Filho & Mittermeier, 1973), Saguinus geoffroyi (Dawson, 1977), S. midas (Thorington, 1968), S. mystax (Castro & Soini, 1977), and S. oedipus (Neyman, 1977). Two species of Saguinus have been seen to form larger groups. Saguinus fuscicollis was observed in groups of either about 10 or between 20 and 40 individuals (Izawa, 1976). The large groups were only seen during the wet season and were suggested to be temporary assemblies of several small groups (families) perhaps associated with seasonal food distribution. The other species, Saguinus nigricollis, was found to live in small groups of eight or fewer individuals consisting of an adult male, an adult female and their offspring. Sometimes two or three of these small groups moved together forming larger groups of 10 to 20 individuals (Izawa, 1978).

Multiple caregiving has been reported in several species. For example adult males have been observed carrying, retrieving and grooming infants in Saguinus nigricollis (Izawa, 1978), S. fuscicollis and S. nigricollis graellsii (Moynihan, 1976), Callithrix humeralifer (Rylands, 1981), and C. jacchus (under the synonym of Simia iacchus, Bewick, 1790).

In order to achieve the aims of this study it was first necessary to collect baseline data on the social development of infants in undisturbed family groups. This constitutes Part I of the study. From these data it was hoped to be able to describe in detail the growth of relationships between infants and other family members, and to suggest a small number of underlying parameters, which, through varying from infant to infant, caregiver to caregiver, and age to age, would explain differences in these infant-caregiver relationships

(see chapter 4). To investigate these parameters further an experimental approach would be required.

The experimental manipulation of social relationships is an area which has largely been neglected. The majority of the work has concentrated on the removal of individuals from groups or mothers, and observations on the changes in the relationships between the removed animals and others on its return from separation or isolation (Hinde, 1977; Suomi & Harlow, 1975). This is effectively the disruption of relationships rather than their manipulation, but it has provided useful information on the strength of mother-infant bonds (Seay et al, 1962), the similarities and dissimilarities of reactions to separation between monkey infants and human infants (Bowlby, 1975; Rutter, 1979), and the variables which affect the nature of infant reaction to maternal separation, e.g. species of subject (Preston et al, 1970), mother-infant relations prior to separation (Hinde & Spencer-Booth, 1970), form of separation (Seay & Harlow, 1962), duration of separation (Harlow & Harlow, 1962), and age at separation (Suomi et al, 1973).

However, separation and the disruption of bonds leads to difficulties in the control of effects on the subject (the infant) from changed relationships with other animals in the group. These changes result from the concomitant disruption of the other animals' relationships with the removed animal (the infant's mother). That is, the whole social nexus is altered by the removal of an animal (Hinde, 1977). A more subtle approach would be to manipulate relationships by altering levels of caregiving behaviour in specific individuals. If this could be achieved there would be minimal alteration to the social nexus and the effects on infant development could be examined under relatively controlled conditions. Using this method parameters suggested to explain infant-caregiver relationships on the basis of the results from Part I of the

study could then be tested by varying particular relationships in specific ways.

It was decided to attempt this manipulation of relationships with the use of a behaviour-modifying drug. Humphreys and Einon (1981) used drugs to alter the social behaviour of young rats in an investigation of play behaviour. The drugs allowed specific items of social behaviour to be depressed differentially, enabling the experimenters to present young rats with potential play partners either exhibiting playful behaviour and/or 'amicable' behaviour (e.g. sniffing and contact) or not exhibiting these behaviours. Drug manipulation of behaviour would therefore appear to be a useful technique which could be extended for use in the present study.

Several different drugs were tested in order to select one which caused an appropriate alteration in the social behaviour of the marmosets without any motor impairment or other measurable side-effects (see chapter 5). All persons involved in the drug studies were in possession of a current Home Office licence and certificate A1.

A second series of observations were then carried out on the social development of infant marmosets, this time with experimentally altered infant-caregiver relationships produced by administering drugs to particular caregivers at particular ages and without direct interference to the infants themselves. This constitutes Part II of the study. From this it was hoped to discover whether the parameters suggested by the results from Part I would allow the prediction of the changes in infant-caregiver relationships that would be produced by the drugs in Part II. If prediction were possible, then the parameters postulated from Part I could be accepted as a reasonable and possible explanation for the distribution of an infant's time and activities amongst its different caregivers and the changes that occur with age.

By these means it was hoped to produce and test a simple hypothesis which would explain some of the complexities of infant social development in a multiple caregiver species in captivity, the common marmoset.

Statement and acknowledgements

No part of this work has previously been submitted for a degree or other qualification to any university or institution.

Some of the data from Part I has been submitted as a paper to the International Journal of Primatology and is in press. This includes sections from chapter 4 dealing with the amount of time infants spend with caregivers, time spent being carried, time in contact, time playing, time grooming, rejection frequencies and frequencies of initiation and termination of bouts of time on.

I would like to thank the following people for help and encouragement during this study:

My supervisor Dr. Neil Chalmers suggested the project, provided help in operating the computer, wrote the original recording programs and made many helpful suggestions.

The Open University animal house staff (Steve Walters, Sharon Prichard and Jacky Campbell) looked after the marmosets and kept them in good condition for the research.

Dr. Ros Ridley (Clinical Research Centre, Harrow) made useful suggestions concerning the drug administration.

The following drug companies provided free samples of tranquillizers for testing: Astra Pharmaceuticals Ltd., Smith Kline & French Laboratories Ltd., May & Baker Ltd., Lundbeck Ltd., and E.R. Squibb & Sons Ltd.

CHAPTER 2 - Colony Maintenance

2.1) HOUSING

The marmoset colony at the Open University is housed in three rooms within the animal unit of the Science Faculty. Room 1 is 3.3m long by 2.3m wide by 2.3m high, room 2 is 3.4m x 2.3m x 2.3m, and room 3 is 3.5m x 3.9m x 2.3m. Room 3 functions mainly as a holding room for adolescent monkeys and newly formed families, while rooms 1 and 2 are used for observational and experimental purposes and contain family groups of monkeys.

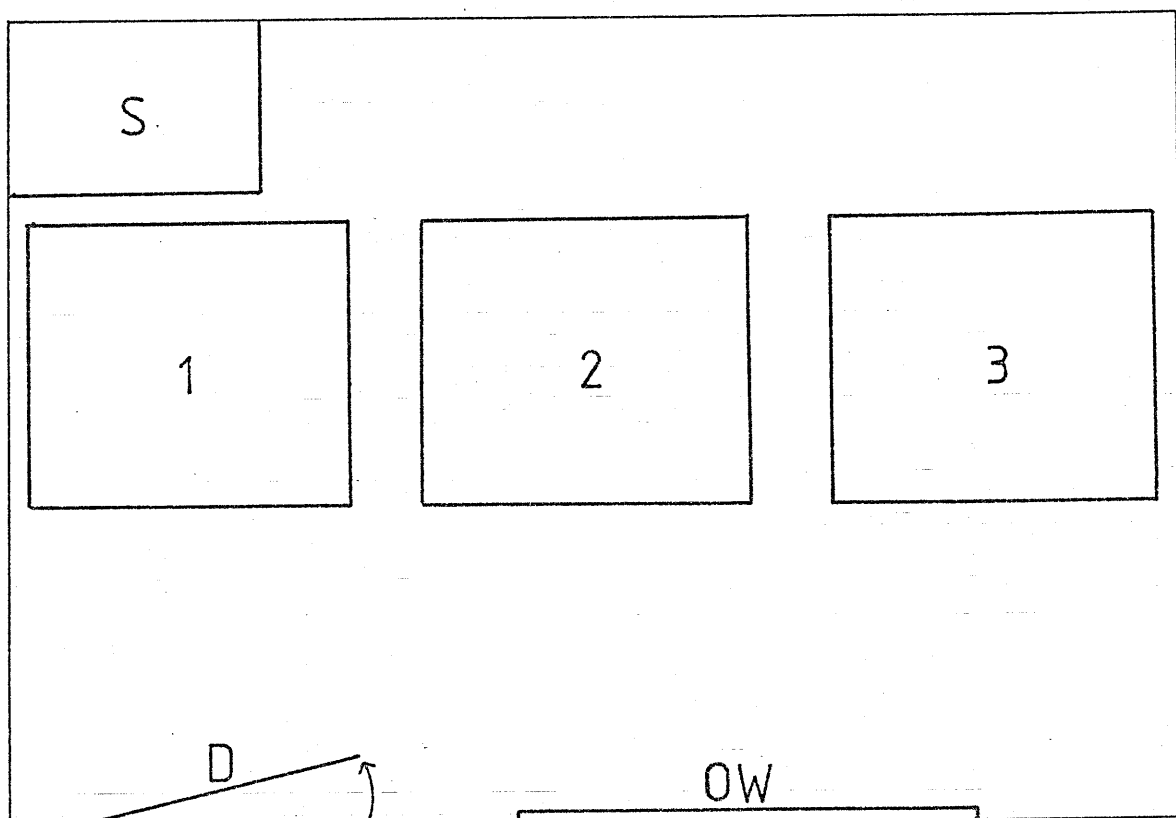
Rooms 1 and 2 each have a 1.2m by 0.5m one-way smoked glass observation window in one wall, the other side of which is a small ante-room from which observations of the animals are made. The one-way windows depend on differential levels of illumination on either side to be effective and the ante-room lights have dimmer switches for this purpose. The windows are kept covered by roller blinds when not in use. The ante-rooms (3m by 1.6m) separate the monkey rooms from the rest of the animal unit. Access to each monkey room is via a door next to the observation window. The micro-computer systems which are used for recording observations are kept on a table in each ante-room.

The third room has two smaller plain glass windows (0.56m by 0.56m, and 0.56m by 0.47m in the inner door), and a small lobby (1.6m by 1.7m) separating it from the rest of the unit and no computer facility and is thus unsuitable for detailed observations or long observation periods. Figures 2.1 and 2.2 show the two rooms used in this study in plan.

Observations for Parts I and II of this study were carried out using room 2. Room 3 was used for the preliminary testing of drugs

Figure 2.1 Plan of monkey room 2. Used for Part I and Part II observations.

For details of family groups see tables 2.1 and 2.2.



KEY

- | | |
|----|--|
| S | : Sink |
| D | : Door |
| OW | : Observation window |
| 1 | : Cage containing family group A |
| 2 | : Cage containing family group B (later group D) |
| 3 | : Cage containing family group C |
| X | : Position of observer in ante-room |

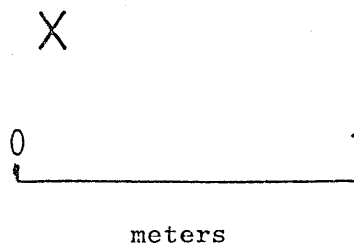
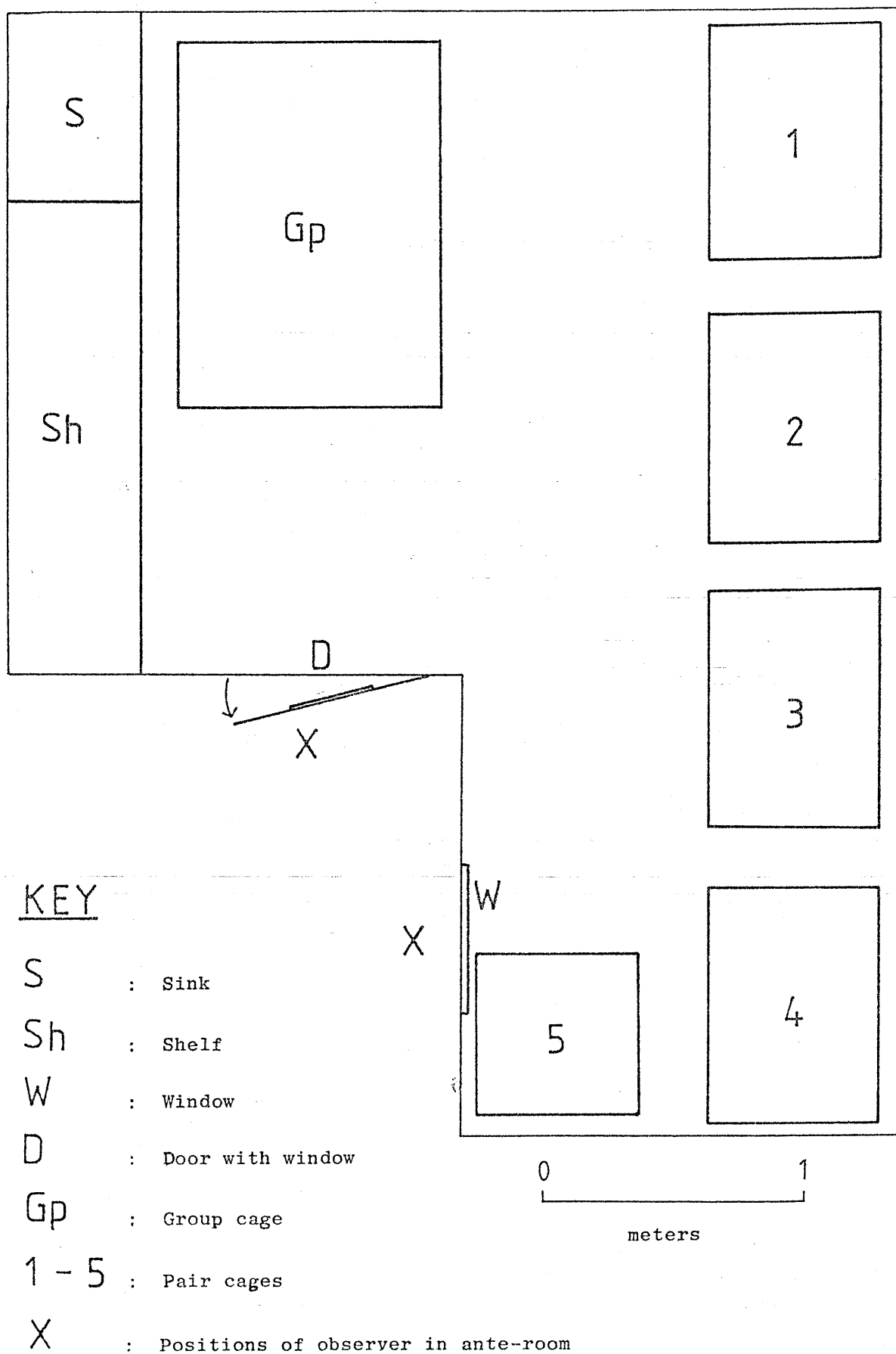


Figure 2.2 Plan of monkey room 3. Used for preliminary drug test observations.



to be used in Part II. Room 1 was in use for another project.

The monkey rooms have no external windows, lighting being provided by two ceiling-mounted 100 watt lights in each room. The lights are controlled by time switches to come on at 6.30am and go off at 6.00pm (Greenwich Mean Time) to give eleven and a half hours of artificial daylight. Marmosets are diurnal and if suddenly plunged into darkness could fall from shelves or perches, as reported by Kingston (1979). To prevent this and to simulate dawn and dusk a twilight period of 30 minutes is provided by dimming the lights before and after the daylight period, i.e. 6 - 6.30am and 6 - 6.30pm.

The dark glass of the one-way windows cuts down the amount of light that can pass through so that the monkey room illumination appears quite low from the observation room. This makes the identification of individual animals more difficult since facial details and colour are less clear. To overcome this and improve observational detail a fluorescent strip light was also fitted in rooms 1 and 2 over the observation windows. These were also connected to the dimmer circuit.

Monkey room temperatures are maintained at $25.5 - 26.6^{\circ}\text{C}$ by means of the building's main central heating system which causes hot air to be blown in through ventilation shafts. The air temperature is set at 21°C in the main system but is boosted to 26.6°C before entering each monkey room. Minimum and maximum temperatures are noted each day and have been found to vary only $2 - 3^{\circ}\text{C}$.

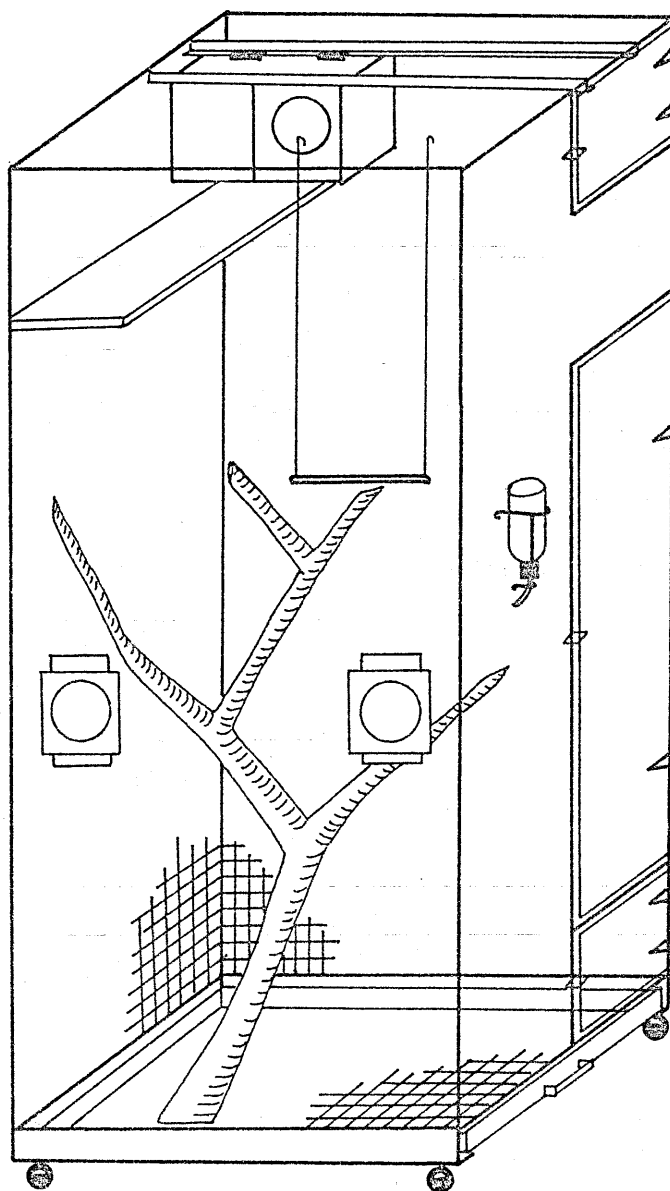
The ventilation system in the roof of the building provides continuous air change for the rooms, with inlet and outlet ducts at ceiling level. The air is filtered before it enters the rooms and as it leaves first by a coarse filter then by a high efficiency filter. Filters are obtained from Vokes Airfilters Ltd., Burnley, Lancashire, and are changed at regular intervals.

High humidity is important since marmosets are susceptible to upper respiratory tract infections and should be maintained at a humidity above 50% (Ingram, 1975b; Stellar, 1960). Kingston (1969) reports that upper respiratory tract infection resulting from too low a humidity is a frequent cause of death in captive colonies. In this colony, the building's main ventilation system is set at a relative humidity of 50%. Each monkey room has a sink and the floor is hosed over each day which assists in keeping the air moist so that the relative humidity is normally between 50% and 60%.

The cages in room 2 (where most observations for this study were carried out) were made in the Open University's Science Faculty mechanical workshop. Each cage is 1.8m high by 0.88m wide by 0.75m deep and made of 2.5cm wire mesh and held together in an angle iron frame. Below the mesh floor is a removeable tray containing sawdust which collects droppings and waste food. The cages are on castors for easy movement during cleaning and are painted black to facilitate observation of the animals inside them which then show up better against the cream coloured walls of the room. Each cage has a 30cm x 19cm x 20cm metal nestbox attached to the roof by runners along which it can be removed. Nestboxes have a 12.5cm x 12.5cm entrance at the side which can be closed by a sliding door from outside the cage to assist in any capture and transfer of animals. Below the nestbox is a shelf and each cage also contains a swing and various branches. Access is by a 44cm by 157cm door which on two cages is subdivided into a larger and a smaller section, each opening independently. There is also a small door for removal of the nestbox, and two circular openings with sliding doors to which flexible tubing can be attached which acts a runway for the movement of animals to other cages if necessary. Figure 2.3 shows one such cage.

Room 2 is large enough to take three of these cages in

Figure 2.3 . Diagram of a family group cage from room 2.
See text for details.



relatively close proximity. Marmosets in captivity appear to be territorial (see Epplé, 1970b and 1972 for Callithrix jacchus, Saguinus fuscicollis and Saguinus geoffroyi). In the wild, some species may be territorial, e.g. Saguinus mystax (Castro and Soini, 1977), S. oedipus (Neyman, 1977 and 1981) and S. geoffroyi (Moynihan, 1970), while others are probably not e.g. S. nigricollis (Izawa, 1978) and Callithrix humeralifer (Rylands, 1981). Because of the possibility of territorial behaviour disrupting family social interactions, large sheet metal screens were fitted on the outside either side of the middle cage to prevent the occupants of each cage constantly being in close visual proximity. Without dividing screens individuals (particularly adult males) become highly excited and threaten occupants of other cages with "erh-erh" vocalizations (a low pitched harsh chattering sound), arch-bristling and staring (see Stevenson and Poole, 1976, for full descriptions of these behaviours). The adult males may also perform genital presenting and give a series of loud, sharp "tsee, tsee, tsee" calls, both of which are considered to be aggressive threat displays by Epplé (1968, 1970b, 1972). Intrafamily aggression also increases. This was seen on occasions when the cages were accidentally left out of alignment. After "erh-erh" calling and arch-bristling at each other for some minutes, two adult males in adjoining cages were seen to turn to other individuals (juveniles or adolescents) near them in their own cages and to bite them aggressively, holding on to the victims tail with their teeth and causing it to scream loudly until released. This level of aggression between family members was only seen after 'confrontations' had occurred between animals in different cages. Every effort was made to try to ensure that cages were correctly positioned thereby preventing this aggression occurring.

Each of these cages holds one family group, that is, an adult

pair and up to two sets of offspring. When the next set of offspring is born into a cage, the eldest set is removed thereby maintaining a constant family composition and preventing overcrowding.

The cages in the other two monkey rooms are of various sizes but are similar in overall design. These were purchased from two commercial suppliers; Forthtech Ltd., Dalkeith, Midlothian, and All-Type Tools Ltd., Purland Road, London.

The floor-tray sawdust is changed and the cages and rooms are thoroughly cleaned once a week using Tego disinfectant, a commercial ampholytic biocidal agent made by Th. Goldschmidt A.G., 43 Essen, Goldschmidt Strasse 100, West Germany. Nestboxes are removed and clean ones supplied every 1 - 2 months and the food bowls and drinking water bottles are washed daily.

2.2) FEEDING AND HEALTH

The diet fed to the marmosets was developed from that given by Stevenson (1976) and consists of the following :

150g of pellet mash is given daily per cage except on Wednesdays, Saturdays and Sundays when fruit is substituted. The mash is made up of 50g of crushed CPDX New World Primate Diet (Labsure Animal Diets, Christopher Hill Group Ltd., Agrarian House, Castle Street, Poole, Dorset) and 50g of meat, i.e. "Chum" and "Pal", canned dogfood made by Pedigree Petfoods, Melton Mowbray, Leicestershire. The meat is to provide additional protein (both animal and plant) since it is known that marmosets have a high protein intake (Clark, 1973; Deinhardt, 1970). Clark (1973) notes that marmosets at Jersey Zoo readily ate calf heart, day old chicks, infant rats, mice, sparrows, and newly hatched ducklings. Occasionally one additional foodstuff (see list below) is

included in the pellet mash.

The standard fruit diet given on Wednesdays and at weekends is made up of 40g each of banana, apple, pear and orange, together with four grapes plus any two additional foodstuffs. This amount is given per cage per fruit day. Additional foodstuffs include :

tomato 40g

hardboiled egg 40g

pineapple 40g

meat 50g

carrot 30g

unshelled peanuts 1 per animal

rusk $\frac{1}{4}$ per animal (Farley's Rusks, Farley Health Products Ltd.,
Plymouth, Devon)

Plus other fruit according to season in similar quantities.

All fruit is chopped up into pieces as the marmosets pick up food with their hands to eat it and will not take very large items (Kingston, 1969).

Water is supplied in a bottle hung on the outside of each cage which provides a continuous flow on demand. Bottles are refilled with fresh water daily. In addition, 50mls of milk made up from instant dried skimmed milk powder is given per adult animal every other day.

As well as the standard diet, various suppliments are given to maintain the health of the animals. Marmosets have a high requirement for vitamin D₃ and in the absence of sunlight are unable to synthesize it from provitamins in the skin. In catarrhine monkeys vitamins D₂ and D₃ may be equally effective in the metabolism of calcium and phosphorus for bone formation. In platyrrhines however, only vitamin D₃ is effectively utilized in bone metabolism. (Hershkovitz, 1977; Lehner et al, 1966). A deficiency of vitamin D in growing animals (D₃ in marmosets)

causes rickets and osteomalacia. Hampton and Hampton (1967) report that the first symptom of rickets seen in young marmosets is the inability to jump. X-rays of these animals show bowing of the long bones, excessive osteoid formation at the joints, bone demineralization and deformity of the lower spine. This condition can be prevented by feeding the animals a supplement of vitamin D₃ provided adequate bone minerals are present in the diet (Clark, 1973; Du Boulay and Crawford, 1968; Kingston, 1969). To this end, 500 iu of vitamin D₃ in 0.5g of powdered glucose is sprinkled on the food of each cage each weekday.

Cytacon, a vitamin B₁₂ solution manufactured by Glaxo Laboratories Ltd., Greenford, Middlesex, is given once a week as 50mls in 500mls of drinking water per cage. 0.6mls of Abidec, a paediatric multivitamin solution (Parke, Davis and Company, Pontypool, Gwent) is given daily per cage, added to the food. 0.5mls of corn oil per adult animal is also given daily with the food to provide a source of linoleic acid which helps to prevent and cure hair loss which occurs periodically in the colony, particularly from the base of the animals' tails. Finally, iodine salt is sprinkled on the food since during a post-mortem of two ten month old marmosets the thyroid gland appeared to be somewhat enlarged.

The food and milk are given in stainless steel bowls placed on the floor of each cage. Food is given at 11am and milk at 4.30pm.

A constant good food supply with no deficiency of vitamins is the most likely cause of the high incidence of triplet births in captive colonies (Ingram, 1975b; Pook, 1976). It has been suggested by Eppler (1970a) that the tendency of captive-bred common marmosets to become much heavier than their parents due to good feeding is connected with hyperfertility and obstetric problems. This colony has experienced very few obstetric problems (see below) but has produced a high proportion

of multiple births - 60% being triplets or quadruplets during the first three years of the colony's existence. However it was considered preferable to have a healthy colony producing extra offspring than to risk trying to reduce multiple births by interfering with the diet.

Infants start to eat solid food taken from the hands or mouths of their parents or siblings at 3 - 4 weeks old and will take their own food from the foodbowl by 6 - 8 weeks. They drink from the water bottle at 5 - 6 weeks. Weaning (i.e. being sustained by solid food and no longer dependent upon milk) appears to be at about 12 weeks of age. This agrees with Ingram (1977) who suggests 11 - 13 weeks. However infants will continue to attempt to nurse as long as the mother lets them even though they may be getting no milk. Juveniles were seen attempting to nurse at 24 weeks old by which time the mother had another set of offspring and was producing milk for them.

Marmosets are susceptible to some human respiratory viruses (Ingram, 1975b; Stellar, 1960) and care had to be taken to avoid infecting them. Labcoats, surgical gloves and paper masks were worn by all people entering the monkey rooms, as were wellington boots so that the wearer could walk through a footbath containing a 1% Tego disinfectant solution placed in front of each monkey room door. Health problems normally reported for marmoset colonies are rickets (see above) and parasites.

Parasites may be found in newly imported animals, or may be picked up from certain food items such as crickets or mealworms (Kingston, 1969; Stellar, 1960). Eppler (1970a) reports that most new arrivals were heavily infected with nematodes and some with acanthocephalans. In Hampton's colony (Hampton et al, 1966), the only major health problem was persistent parasitism. They noted infestations

of microfilaria, trypanosomes, metastrongyles, cestodes, and the acanthocephalan Prosthenorchis elegans. Kingston's (1969) problems included Prosthenorchis which employed coleopteran larvae as the intermediate host, and an outbreak of Shigella transmitted from inadequately quarantined new stock which caused a large number of deaths.

Hunt et al (1978) review the infectious diseases which may be found in marmosets. They list four types of Herpesvirus, also measles, rabies, yellow fever, paramyxovirus enterocolitis, tuberculosis, shigellosis and salmonellosis. Other bacterial diseases include pneumonia and meningitis caused by Diplococcus pneumoniae, purulent inflammation from Staphylococcus and Streptococcus spp., enteritis from Escherichia coli and Proteus spp., pseudotuberculosis from Yersinia enterocolitica and enteritis, pneumonia and septicemia from Klebsiella pneumoniae.

Of parasites, the most important is the acanthocephalan Prosthenorchis elegans. The proboscis of this 'thorny-headed' worm becomes buried in the wall of the ileum, caecum or colon leading to ulceration and abscess formation. The outcome of infestation is often mesenteric lymphadenitis, peritonitis and death from septicemia. There is no known safe and effective treatment and individual worms may have a lifespan of several years. Prosthenorchis spirula also occasionally causes this condition. Other parasites which may be found include various trematodes, cestodes, nematodes and protozoans.

All the original members of this colony had spent several years in other captive colonies (all but one being born there) and had been cleared of parasites before they arrived at the Open University. They were fed only prepared food and showed no signs of harbouring parasites. Faecal samples were periodically taken and sent to Cherwell Laboratories Limited (Murdock Road, Bicester, Oxfordshire) for analysis

but no evidence of parasites was found.

Very few problems were encountered in this colony, and all so far have been successfully treated or have spontaneously recovered. One animal, an adult female, appeared to "catch" a common cold virus and had runny eyes and nose and repeatedly sneezed. A decongestant ointment (Vick, made by Richardson-Merrell Ltd., Consumer Products Division, Slough, Bucks.) was administered and the animal returned to normal within six days. Another adult female developed a raw sore patch on her neck where her identification necklace had been rubbing. The necklace was removed and the sore treated with Savlon antiseptic cream (Avlex Ltd., Macclesfield, Cheshire) and Aureomycin, a 2% chlortetracycline hydrochloride powder manufactured by Cyanamid of Great Britain Ltd., Animal Health Division, Gosport, Hampshire.

The canine teeth of an old (about eleven years) male had grown particularly long and appeared to be pressing against his lips and causing pain. The teeth were removed by a veterinary surgeon while the animal was under general anaesthetic (halothane). Before removal, the male had been particularly aggressive and had bitten off half of the tail of one of his ten day old infants. The infant was removed from the cage so that the tail stump could be sprayed with Nobecutane, a transparent acrylic resin dressing (Astra Chemicals Ltd., Watford, Herts.) and dusted with Aureomycin. It healed perfectly and the monkey, now adolescent, appears to suffer no serious locomotor impairment.

Hair loss, particularly from the base of the tail, was quite common before the introduction of corn oil into the diet. Animals who still occasionally show it are treated with Aureomycin and Vetsovate cream (a steroid cream for skin disorders made by Glaxovet Ltd., Greenford, Middlesex) and the hair rapidly regrows.

Out of the 39 births which took place during the first three

years of the colony's existence, there have been only two with complications, both of these from the same female. In the first instance, the birth took place on a Sunday morning and was observed intermittently by a technician. The female apparently had great difficulty in delivering triplets, the second infant, and possibly the third, being in the breech position. Two of the three infants died shortly after birth, and the female bled profusely for three days. She appeared weak and listless but after a week had returned to normal. The infants had not been especially large, the surviving one weighed 35g at two weeks old (the mean of 11 other two week old infants, 9 of whom were also triplets, was 38.5g, standard error 2.98), but this adult female was a particularly small, slim animal and had only previously produced singletons and twins. She weighed 376.6g at 5 years old, compared with a mean for all six adult females at roughly the same stage of pregnancy of 403.6g, standard error 9.9, age range 4 - 6 years. Her next two sets of offspring, one of triplets and one of twins, were produced without difficulty but the following set of triplets again caused problems. All three infants were found dead on the day of birth and the female appeared weak and was bleeding quite heavily. After two days she was much stronger though still losing blood, and after a week she seemed quite recovered. This birth was towards the end of the study and the family was not used to produce any more subjects. Unfortunately, the set of triplets which died contained an infant which was due to become one of the subjects for Part II.

The final health problem encountered so far in the colony concerned an adult male who became seriously ill with what was presumably an intestinal infection. He had difficulty in swallowing, was unable to retain any food and lost weight rapidly. Blood samples and a barium meal X-ray taken by a veterinary surgeon gave no clues as to the

cause. The animal was separated from his family, kept on a liquid diet and given a course of penicillin. After four weeks he seemed improved and could take small amounts of soft fruit. He gradually recovered his health after a further month of separation from his family. Separation was necessary as the rest of his family would not allow him to feed without interruption and he was too weak to chase them away.

Unfortunately this male was the father of one of the family groups under observation for this study (group B, see section 2.4)). As soon as the illness was detected watches were abandoned on the infant in that cage and the whole family was moved to room 1. A family from room 1 (group D) was then moved to room 2 as a replacement. The female of this group gave birth shortly afterwards and observations could continue on a new infant. This was a necessary move in order to obtain data on enough individuals in the time available.

As a result of this experience, rectal swabs were taken of all animals (other than infants) in the colony and sent to Cherwell Laboratories Limited for bacteriological examination. Cultures made from the swabs showed that all animals harboured non-pathogenic Escherichia coli and Proteus mirabilis. Some animals had an unspecified Klebsiella species which could cause illness if the animals became stressed. It seemed likely that this organism had been the cause of the adult male's illness, but suprisingly the swab culture of the male did not show this up. There was no evidence of Salmonella or Shigella in the colony.

As the colony is now several years old it may soon begin to experience problems associated with aging. The adult male whose canines became elongated and deformed is one example and other males are beginning to show signs of irregular teeth. Other problems which could be expected in the future include impaction of the caecum, colonic diverticulitis, chronic nephritis, muscular wasting and infections of the claws and nails.

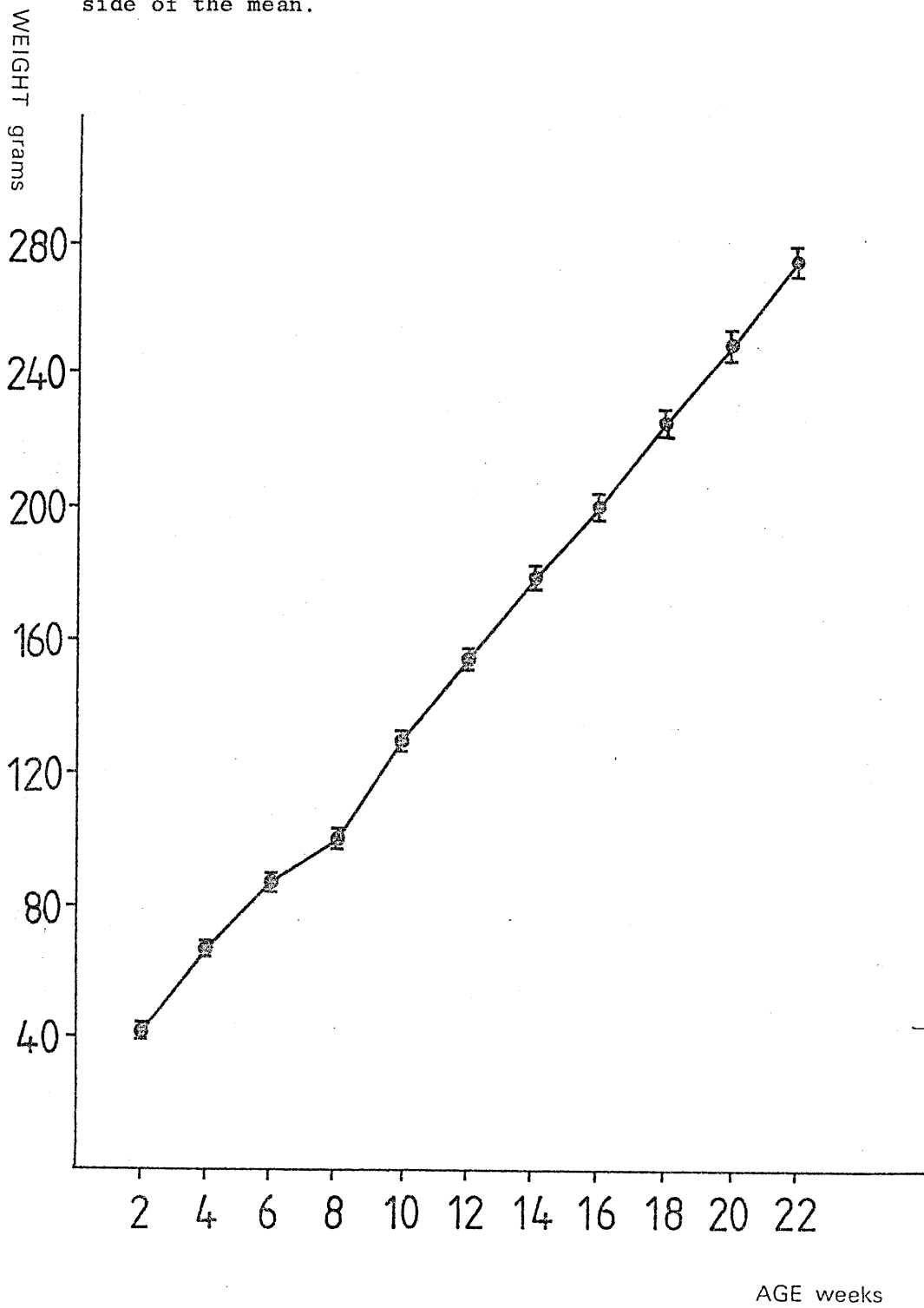
2.3) HANDLING AND HANDREARING

Monkeys had occasionally to be handled for purposes of weighing, marking, drug administration and treatment of minor injuries. In all cases handlers wore long leather gloves since marmosets will bite but their small teeth cannot easily penetrate thick leather. Animals were either grasped directly using the gloves, or in the larger cages trapped with a butterfly net first.

For weighing, animals were transferred to a small (240cm x 190cm x 140cm) wire mesh cage which could be placed on a Mettler PK 16 electric balance which weighs continuously. Infants used as subjects in this study were weighed every two weeks, though they only had to be caught for the first eight weeks. After this they effectively weighed themselves on a device which could be hung temporarily in the cage. Any new object in a cage attracts a great deal of attention, particularly from young animals who will confidently explore and swing on objects hung from the cage roof. In this case, a section of a wire mesh wild bird peanut feeder was attached to a Salter 12 500g maximum spring balance and the whole was hung from the cage roof. As each infant hung from the mesh basket, its weight could be fairly accurately (within 5g) read off from behind the observation window. Figure 2.4 shows the mean weight of 16 infants used in this study. Infants' fortnightly weights were compared against the mean at that age to check whether or not they were growing at the expected rate.

All the adult animals in the colony were distinctively different from each other in facial characteristics. Most adolescents could also be distinguished with familiarity and practice. However, in this study, infants had to be individually identified as early as two weeks of age. At this age twins usually appear more or less identical

FIGURE 2.4 Mean weight of 16 infant common marmosets weighed at fortnightly intervals. Bars represent one standard error either side of the mean.



so some method of marking individuals was necessary. This was also required to a certain extent for older animals since during the sometimes extremely rapid interchanges of behaviour, for example in play, an individual's identity had to be immediately obvious or recording of the timing of events would become inaccurate. Some of the adult animals obtained from other colonies arrived wearing small chain necklaces with either numbered metal discs or coloured plastic rings attached for identification. This method of marking has problems in that chains have to be constantly checked against rubbing and replaced as the animal grows, necessitating frequent handling. One adult female developed a sore patch on her neck from the chain rubbing (see section 2.2)) which had to be removed. In addition, this is unsuitable for very young infants who do not have a well defined 'neck' to place a chain around.

An alternative method is to paint the animal's fur with a dye or stain. Several commercial sheep dyes were tried but these lasted no more than a few days as frequent grooming of the marked animals rapidly removed all traces of colour. Eventually a weak solution of picric acid was used. This dries leaving a bright yellow stain which can last several months. Picric acid (2,4,6-trinitrophenol) is stored under water for safety since on drying out it becomes highly explosive. By decanting off this water from a stock bottle of picric acid (and immediately replacing that taken with fresh water) a solution was easily obtained which would be adequate for several month's use. Casual observations of marked animals suggested that this treatment led to no apparent alterations in their behaviour, or of the behaviour of other animals towards them. This was confirmed by the analysis by caregiver of the behavioural data collected (see chapter 4). In fact the monkeys did not appear to notice the yellow stain, and did not stare or groom to remove it as they did the blue and red sheep dyes. Infants (subjects)

were marked on the head when they were caught for weighing and from the last capture at eight weeks a noticeable difference in head coloration between the twins (one marked, one unmarked) generally lasted until the end of the study period for that infant at 22 weeks old. Older animals (siblings of the subjects) were marked if necessary on the otherwise white ear tufts which begin to appear at around five months old.

Because, in this study, the infant subject from one offspring set becomes one of the older siblings to the next infant subject from that family (see section 2.4)), there was always one older sibling who had been handled for weighing and marking when an infant. This sibling is designated 'sib 1' in what follows, to distinguish it from its twin 'sib 2' which had not been handled and had not been a subject.

Handling required during drugging procedures is described in chapter 5.

Triplet births were common in this colony (20 out of a total of 38 births from 1978 to 1981) and as families can only raise two infants at a time (see section 2.4)) it was decided to try to handrear third infants. Although these could not be reintroduced to their families if they were involved in behavioural observations it was hoped that they could eventually be housed in room 3 with the other adolescent and 'spare' animals. The method followed for handrearing was that set out in Stevenson (1976). Infants were kept in 'Curfew' chick incubators (Curfew Appliances Ltd., Ottershaw, Surrey) at 30 - 35°C. A sheet of hessian was laid in the bottom and a tray of water kept beneath to maintain high humidity. A piece of synthetic fur material was used as a surrogate mother for the infant to cling to. Although attempts were made to handrear eight infants, only two survived to maturity. The other six died at 4, 5, 6, 8, 43 and 56 days respectively, the last two of bacterial infections. Other workers also report a low success

rate for handrearing infants (Hearn and Burden, 1979; Pook, 1976).

Another method of raising triplets is discussed by Hearn and Burden (1979). Handrearing techniques are applied to each offspring in turn so that none is wholly deprived of marmoset family care. Each infant is removed at 9 a.m. and kept in a paediatric incubator for 24 hours, then swapped for another. By this means all three offspring of triplet births can be successfully reared to weaning. This method would be inappropriate for this colony since it would involve too much interference and handling of families which should ideally be in an undisturbed state for behavioural observations. Secondly, families with triplets would have an 'extra' infant, this would create problems in recording observations due to the layout of the computer keyboard involved (see chapter 3), and infant subjects would then not all be matched for family composition as far as possible.

Due to the low success rate of attempts at handrearing and the considerable amount of time and effort it involves, it was decided to maintain offspring set size at two individuals by removing and humanely killing any extra infants. These infants were removed on either the first or second day of life and given an overdose of the anaesthetic Sagatal (pentobarbital sodium, manufactured by May and Baker Ltd., Dagenham, Essex). One millilitre of the 60 mg/ml solution was injected intraperitoneally. Before this procedure started no family had been able to raise more than two infants from a set, the remainder always dying before they were five days old.

2.4) COLONY COMPOSITION AND SUBJECTS USED.

At the start of this study in 1979, the marmoset colony consisted of six adult pairs and the offspring they had produced since

the colony was founded a year before, a total of 26 animals. The adult animals had been obtained from the Psychology Department of Reading University and the Zoology Department of the University College at Aberystwyth. They were housed such that pairs were formed between animals from the two different sources as far as possible.

Adult pairs are kept in family cages containing up to six animals, that is, the parents plus two sets of offspring. When the next set of offspring is born, the eldest set who are now approximately ten months old, are removed thereby preventing overcrowding. Thus, except in the few cases of singleton births, an infant is always a member of a group containing its twin, a pair of siblings approximately five months older (since births are at roughly five month intervals, see below), its mother and its father. The offspring removed at ten months are transferred to room 3 and housed initially as pairs of twins or placed in a large cage with up to three other twin pairs. When sexually mature they are either sold or used to form new adult pairs.

In captivity, adult female marmosets commence cyclical ovarian activity immediately after parturition and may become pregnant on the first cycle after giving birth, i.e. within about ten days, and may give birth every 5 - 6 months (Hearn, 1977). Other sources give similar interbirth intervals for captive marmosets, for example six months (Kingston, 1969), about 150 days (Rothe, 1977), and 151 - 156 days (Stevenson, 1976). This seems to follow the pattern which has been observed in the field; Eisenberg (1977) states that "Callitrichids" give birth every six or twelve months in the wild. More specifically, Callithrix humeralifer in Brazil has two breeding peaks a year with five months between the peaks (Rylands, 1981), Saguinus nigricollis in Colombia gives birth twice a year in June and December (Izawa, 1978), and observations of Saguinus fuscicollis in Peru suggest births occur

twice a year (Castro and Soini, 1977).

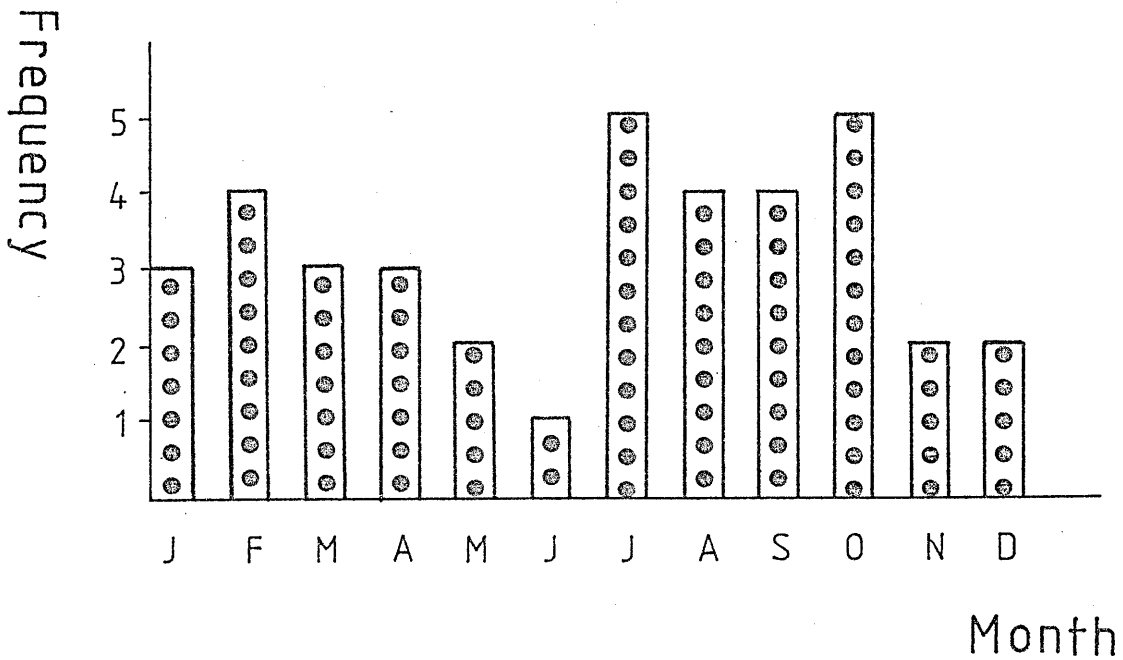
In this colony, the mean interbirth interval of 27 births was 159.37 days, with a standard error of 3.60. Mating was first observed between 4 and 29 days after parturition (mean 14.5 ± 2.79 days) but first matings may have been missed since the animals were not watched continuously. Hearn and Lunn (1975) report that common marmosets mate 3 - 10 days after giving birth, Epplé (1970a) gives 7 - 10 days, and Stevenson (1976) 8 - 11 days post partum for most frequently observed matings. This gives an estimated gestation length for this colony of around 145 days. This agrees well with other colonies estimates of 140 - 150 days (Epplé, 1970a), 140 days (Kingston, 1969), and 141 - 146 days (Stevenson, 1976), all for Callithrix jacchus, and 140 days for Saguinus oedipus (Hampton and Hampton, 1965). Hearn, (1977) determined the gestation period for common marmosets physiologically by luteinizing hormone assay and found it to be 148 ± 4.3 days.

Common marmosets normally produce dizygotic twin chimeric young as a result of placental anastomoses (Hearn, 1977) though triplets are not uncommon in captivity. (Epplé, 1970a; Stevenson, 1976). The incidence of triplets has a tendency to increase from the time of the establishment of the colony. In Hearn and Burden's (1979) colony, the percentage of all births which were triplets increased steadily from 12% in 1974, 18% in 1975, 28% in 1976, to 43% in 1977. In this colony, from October 1978 to October 1981, out of 38 births 7.89% were singletons, 31.58% were twins, 52.64% were triplets and 7.89% were quadruplets. Hearn's finding that the incidence of triplets increased with colony age is in line with data from this colony which suggest that females' first births tend to contain fewer offspring than subsequent births. Of the three singleton births which occurred, two were first births and the other the second birth by a female.

Where more than two offspring were born at a time, the remainder, if left with the family, died within five days of birth. Stevenson (1976) also reports that families seem unable to rear more than two infants at a time and suggests that the female does not produce enough milk to maintain all three. Mothers were observed to nurse infants two at a time (see also Ingram, 1975a; Kingston, 1969) so if there are more than two the weakest will miss out on some feeds. Hearn and Burden (1979) suggest from unpublished observations that the main intake of milk is probably at night, and as the female spends the night with two infants attached to her nipples, the remaining triplet declines rapidly. Eventually it becomes too weak to cling on to a caregiver and falls to the cage floor to die of starvation or hypothermia. Parents were seen to attempt to retrieve fallen infants but if they repeatedly fall off the caregiver they are eventually left and die. For this reason, if more than two infants were born in any offspring set, the excess were removed on the first or second day of life and killed with an overdose of anaesthetic (see section 2.3)).

Seasonality of births was not observed. Figure 2.5 shows the number of births which occurred during each month from October 1978 to October 1981 and it can be seen that, apart from brief 'lows' in June and November/December, births were fairly evenly spread out across the months of the year. There was no statistically significant difference in the frequency of births in each month (χ^2 one-sample test, $\chi^2 = 5.525$, $p > 0.9$). Lack of birth seasonality seems to be generally true for common marmosets in captivity (see Epplé, 1970a; Hearn, 1977; Ingram, 1975a; Kingston, 1969), though the cotton-top tamarin (Saguinus oedipus) shows a slight grouping of births in spring and autumn (Hampton and Hampton, 1965; Hampton et al, 1965). A recent study in captivity (Brand, 1980) showed that of five callitrichid species (cotton-top

Figure 2.5 Seasonality of births in the colony. Frequency of births occurring in each month from 19/10/78 to 14/10/81. N = 38.



tamarins, silvery marmosets, common marmosets, Goeldi's monkeys and red-mantled tamarins) only the cotton-top tamarin exhibits a seasonal influence on birth distribution with most occurring in spring and least in summer.

Gartlan (1968) has suggested that some species of primates display breeding cycles in correlation with environmental factors in the wild, while they mate at any season in captivity. This would appear to be related to the constancy of environmental conditions generally occurring in captivity. Confirmation of this is provided by Coimbra-Filho (1965) who kept Leontopithecus rosalia in outdoor enclosures in Rio De Janeiro and found births occurred from September to January, i.e. the Brazilian spring and summer. Field workers have found birth seasonality in wild populations of marmosets, for example Callithrix

humeralifer has two breeding peaks, one at the beginning of the wet season (September to November) and one during the middle of the wet season (February to April) (Rylands, 1981).

Thirteen infants in family cages died from 19/10/78 to 27/9/81. This was before regular over-anaesthetizing of third infants had begun and all of these were the excess infants from multiple births. In addition, a pair of twins born to one female in room 3 died at 35 and 43 days respectively. These were the product of a mating between a brother and sister caged together beyond the age of sexual maturity. Epplé (1970) also reports the occurrence of a brother/sister mating and birth but gives no further details. The female was paired with another unrelated male 34 days before the infants were born and it is quite likely that they were attacked by either the male or their mother as one was found with its tail partly bitten off and the other had its tail completely removed. They presumably died from loss of blood. Tail-biting had also occurred in room 2 when an infant had half of its tail removed as noted above in section 2.2), though this infant was treated immediately and survived. A similar occurrence is given by Pook (1976). In his colony two handreared infants were replaced in their parents' cage at 39 days of age for half an hour to an hour a day to prepare for their complete reintroduction to their family. The parents apparently accepted them during these short reunions but after a week of this one infant was found with its leg being chewed at by one of its parents, and had half of its other leg and half its tail missing.

From the original six pairs, the colony has produced to date (19/10/81) 99 animals. This is a higher rate of production than could be expected in the wild. Neyman (1981) suggests that the output of young per female Saguinus oedipus in the wild is less than ten young born in her lifetime. The females in this colony have so far produced a mean of

16 \pm 1.65 young each and there is no reason to suppose that they will not continue to reproduce at the same rate for at least another five years. The difference in productivity is most likely related to the constant food supply and lack of predators and disease in captivity.

Observations for Parts I and II were carried out in room 2 and were thus limited to the families present in the three cages in this room. The project was designed such that for Part I there would be nine subjects, three infants from each of the three families, and the same for Part II. This would allow comparisons of family differences to be made across the two parts, as well as an equal number of subjects in the undisturbed and in the drugged conditions. Data was recorded for nine subjects in Part I. However, as noted in 2.2) above, the illness of one of the adult males necessitated exchanging his family with another healthy one from room 1, such that Part II contained some subjects from a family relatively new to the room compared with the other families used. In fact the female gave birth shortly after the move so that the subjects taken from that family had spent their entire lives in this room, though the parents and one set of older siblings had previously been in room 1. Data from the infant which was being observed when the father became ill was discarded.

Unfortunately it was impossible to obtain data on nine infants for Part II as the last set of infants to be used from one of the families were all found dead on the day of birth (see section 2.2) above). There was insufficient time left available to wait another five months for another set to be born (or another ten months to ensure older siblings of an equivalent age to all other subjects' siblings), and no other families were readily available to be moved into room 2 as a replacement. This resulted in there being only eight subjects for which data was collected in Part II.

The subjects used consisted of one infant from a pair of twins from each successive set of offspring available. Each pair of twins became the older siblings to the next pair of twins born to their family, so that each subject was in fact observed over two time periods, once as an infant subject, and once as a caregiver to the next infant subject. In what follows, subjects are referred to as 'infants' even though they are observed up to 22 weeks of age, by which time they can be classified as juveniles (Ingram, 1975a). Male and female parents are referred to respectively as the 'father' and the 'mother' the infants littermate is referred to as its 'twin', and the remaining family members who are the previous set of offspring as 'siblings' or 'older siblings'. As noted above (see section 2.3), the sibling which was the subject in the previous set of infants is referred to as 'sib 1' and its twin as 'sib 2'. Of the nine subjects used in Part I, seven were male and two female. In Part II, two out of eight subjects were male and six female. Tables 2.1 and 2.2 give details of the families and subjects used. After section 4.5b) siblings are no longer distinguished as sib 1 and sib 2 but are both simply referred to as siblings.

Table 2.1

Marmoset families used in the study.

Family code	Source of parents	Age of parents at start of study/years	No. litters produced before start of use in this study	No. subjects provided
A	♂ Reading	4½	2	6
	♀ Aberystwyth	3		
B	♂ Reading	4	2	4
	♀ Aberystwyth	3		
C	♂ Aberystwyth	> 8	2	5
	♀ Aberystwyth	2½		
D	♂ Aberystwyth	2½	5	2
	♀ Reading	2½		

Family B - Father became ill, family removed.

Family D - Family which replaced family B.

Family C - Eighth litter containing ninth subject for Part II all died on day of birth.

Subjects used in the study.

First line - ringed symbol gives sex of subject
 xn gives litter size, x2 = twins
 x3 = triplets
 x4 = quadruplets
 second symbol gives sex of twin.

Second line - symbols give sexes of older siblings. A ringed symbol indicates sibling was a subject in the previous litter.

FAMILY		A	B	C	D
SUBJECT					
Part I	1		♂ x3 ♂ ♀ ♀		
	2			♂ x2 ♀ ♂	
	3	♀ x2 ♂ ♀ ♂			
	4		♀ x3 ♂ ♂ ♂		
	5			♂ x3 ♂ ♂ ♀	
	6	♂ x3 ♂ ♀ ♂			
	7		♂ x3 ♂ ♀ ♂		
	8			♂ x3 ♂ ♂	
	9	♂ x3 ♂ ♂ ♂			
Part II	1		♀ x4 ♀ ♂ ♂		
	2			♂ x3 ♀ ♂	
	3	♀ x3 ♀ ♂ ♂			
	4			♀ x2 ♀ ♂ ♀	
	5				♀ x3 ♂ ♀ ♂
	6	♂ x2 ♀ ♀ ♀			
	7				♀ x2 ♂ ♀ ♂
	8	♀ x3 ♂ ♂ ♀			

CHAPTER 3 - Methods

This chapter describes what particular behaviours were observed and recorded, how the data were collected and how they were organised for presentation and analysis.

3.1) BEHAVIOURS OBSERVED

The object of this study was to investigate relationships between individuals, hence data was collected on social behaviour. Non-social behaviour, such as gnawing and manipulating objects, was not required. Preliminary observation of marmoset families had allowed a comprehensive list of interactive behaviours to be drawn up and data was collected on these. The behaviour categories used in this study are defined below and are listed in table 3.1. Alternative names used to describe behaviours are given in the definitions. Names for behaviour categories are used throughout the text as shown below, i.e. without quotation marks, underlining or capital letters unless indicated below.

a) Behaviour states.

A 'state' is a behavioural category which lasts for a measurable amount of time which is delimited by the moment it begins and the moment it ends. Seven separate states were recorded, four of which are mutually exclusive, while the remaining three overlap in time with two of the first four (see table 3.1). An eighth state combines five of the separate states. States are recorded for the subject infant with respect to the caregiver it is interacting with. For example an infant playing with it's twin is recorded as being in a state of play even though it is

Table 3.1

Behaviour categories used in the study.

A. STATES	i) Mutually exclusive
	1. On
	2. Contact
	3. Huddle
	4. Off
	ii) Overlap with 3. and 4. above
	5. Play
	6. Infant grooms
	7. Caregiver grooms
	iii) Combined
	8. With

B. EVENTS	i) Recorded at all ages
	1. Infant is picked up
	2. Infant avoids carry
	3. Infant gets on
	4. Rejection
	5. Infant gets off
	6. Caregiver restricts
	7. Rub-off
	8. Fails to rub off
	9. Approach
	10. Leave
	11. Successful food-steal
	12. Unsuccessful food-steal
	13. Threat/attack
	14. Tantrum
	15. Ignore
	ii) Recorded at 22 weeks only
	16. Successful, interruption
	17. Unsuccessful interruption
	18. Picks up infant sibling successfully
	19. Picks up infant sibling unsuccessfully
	20. Rubs off infant sibling successfully
	21. Rubs off infant sibling unsuccessfully

also off (i.e. away from, see definition below) it's parents and siblings.

i) On

Time on is defined as being the period during which an infant is being carried by a caregiver. The infant may be carried in any position (dorsal, lateral etc.) provided that if the caregiver moves away the infant is carried along with it. Infants which are on maintain their position by clinging with hands and feet and are not held on by the caregivers themselves.

ii) Contact

Contact is described as an infant sitting with a specific caregiver. That is, the infant sits, crouches or lies next to another individual with some part of its body touching the other, and with its trunk within 20 cms of that individual. Usually contact involves animals sitting alongside each other pressed closely together. Contact only involves two animals at a time, the infant and one caregiver. Where more than two animals are involved the behaviour category becomes huddle (see below).

iii) Huddle

Huddle, or family huddle, occurs when more than two animals are sitting together as above. It usually occurs for prolonged periods and often involves all animals in a cage forming a heap. Their tails frequently coil up and they may sleep intermittently.

iv) Off

Time spent off is equivalent to that time when the animal is in none of the above three states. That is, it is not on caregivers or in contact with them but is away from them by at least 20 cms.

v) Play

Play for the purposes of this study includes social play only. Self-play, or play with objects is not included. Play is typically silent and may involve the play-face or open-mouth face (Stevenson &

Poole, 1976). It consists of rapid chasing with frequent to-fro motions between the animals, pouncing and wrestling, rolling, gentle biting, grasping and batting. Social play in common marmosets is more fully described in Chalmers & Locke-Haydon (1981).

vi) Infant grooms caregiver.

Bouts of allogrooming in which the infant grooms another individual, combing through the fur with its hands and nibbling with its teeth.

vii) Caregiver grooms infant.

Bouts of allogrooming in which the infant is groomed by another individual. Categories vi) and vii) often occur alternately but the situation where two animals groom each other simultaneously does not occur.

viii) With

Time with is a combined behaviour state made up of the sum of time spent on, in contact, playing, grooming and being groomed. It is thus a measure of the total time an infant spends within 20 cms and interacting with an individual.

A different way of measuring time with would be the total time spent between approaches and leavings with that caregiver (this has been termed time in proximity in section 3.3) and in chapter 5). However, time with and time in proximity overlap to different degrees at different ages and it was not possible to entirely separate them out in the early weeks of infant life from the data collected. For example, time in proximity depends on the occurrence of an approach and then a leaving. In the first few days of life an infant may be passed from one caregiver to another (via a rub-off and then a pick-up by an adjacent caregiver) without an approach or a leave occurring. This is recorded as time with but not time in proximity. Hence time with was chosen in preference to time in proximity

as a measure of overall distribution of infant time amongst it's caregivers.

b) Behaviour events.

An 'event' is a behavioural occurrence for which a duration measure is not taken, for example an approach. Most events occur instantaneously, though even with longer events (such as an attempt by a caregiver to rub an infant off which fails) it is assumed that it is the occurrence of the event which is important not how long it takes.

i) Infant is picked up.

An initiation of a bout of time on by a caregiver, also described as a caregiver 'on', where an 'on' is an initiation of a bout of time carried (in this case by a caregiver rather than by an infant). The caregiver leans towards the infant and may stretch out an arm towards it. The infant responds by clinging on to the caregiver. Sometimes the caregiver may grasp the infant with one or both hands.

ii) Infant avoids carry.

The infant avoids being picked up and carried by a caregiver. In this case a caregiver attempts to pick up an infant but the infant does not respond by clinging on to it. The infant may move away from the caregiver or simply remain where it is.

iii) Infant gets on.

A bout of time on initiated by the infant, also described as an infant 'on'. The infant crawls or climbs on to a caregiver without any assistance from the caregiver.

iv) Rejection.

A caregiver prevents the infant from climbing on to it either by moving away from it and pushing it away, keeping it at a distance with an arm, or by lunging at it and biting it while making 'erh-erh' vocalizations (Stevenson & Poole, 1976).

v) Infant gets off.

The termination of bout of time on by the infant, also described as an infant 'off', where an 'off' is a termination of a bout of time on (in this case by the infant rather than by a caregiver). The infant climbs off the caregiver apparently of its own accord.

vi) Caregiver restricts.

A caregiver prevents the infant from getting off of it, by pulling it away from the part of the cage it was about to move to, or by obstructing it with an arm.

vii) Rub-off.

A rub-off is the termination of a bout of time on by a caregiver, also described as a caregiver'off'. The caregiver scrapes the infant off through rubbing it against the side or floor of the cage. Rubbing-off may involve the infant's hands, feet and head being bitten while it is pushed against the cage, and caregivers may also attempt to push infants off with their hands.

viii) Fails to rub off.

A caregiver attempts to remove an infant it is carrying by rubbing it against the cage, but the infant prevents itself from being rubbed off, often by crawling over the caregiver away from the region that is being rubbed.

ix) Approach.

An approach is any movement by an individual towards another individual which brings it from beyond 20 cms to within 20 cms of that individual. The distance of 20 cms was chosen as being approximately the reaching distance of a marmoset other than a small infant.

x) Leave.

The reverse of an approach, that is, any movement by one individual which takes it beyond 20 cms of another individual.

xi) Successful food-steal.

The infant takes a piece of food from the hand or mouth of a caregiver.

xii) Unsuccessful food-steal.

The infant tries to take a piece of food from the hand or mouth of a caregiver but does not succeed in obtaining it.

xiii) Threat/attack.

A caregiver threatens the infant by sitting up on its haunches, flattening its ears and making 'erh-erh' vocalizations. An attack occurs when the caregiver lunges at, or chases the infant, grasping it with one hand and biting it hard. This category of behaviour usually occurs when older infants try to steal food from caregivers.

xiv) Tantrum.

A distress call, the "characteristic infantile reaction to loss of physical contact" (Epple, 1968) made by infants usually during the early weeks of life when they are left alone or are roughly handled by their caregivers. Epple (1968) describes the sound as a squeal or 'ngä' call. Tantrums tend to get harsher in sound as the infant gets older.

xv) Ignore.

A caregiver ignores the infant's attempt to gain its attention. for example the infant may approach a caregiver and vocalize, but the caregiver does not move or turn to look at the infant.

All the above behaviour categories were recorded at all watching ages. The following behaviours were recorded at 22 weeks of age only as part of the social competence score (see chapter 4).

xvi) Successful interruption.

A successful interruption occurs when the action of one individual causes another individual to cease what it is doing and do

something else. For example, an animal jumping on or batting another to start it wrestling, or lying down in front of it to elicit grooming, or interfering with it eating or drinking such that the other animal moves off.

xvii) Unsuccessful interruption.

A potentially disruptive action by one individual which fails to cause another individual to cease the activity it is engaged in.

xviii) Picks up infant sibling successfully.

The infant picks up and carries a member of the succeeding set of offspring born into its family when it is about five months old, i.e. it's own infant sibling.

xix) Picks up infant sibling unsuccessfully.

The infant tries to pick up and carry an infant sibling, but fails as the baby does not respond to its attempts but remains where it is.

xx) Rubs off infant sibling successfully.

The infant terminates a bout of carrying of an infant sibling by rubbing it off.

xxi) Rubs off infant sibling unsuccessfully.

The infant tries but fails to rub off an infant sibling it is carrying.

3.2) RECORDING OF OBSERVATIONS

a) Watching schedule.

A focal-animal sampling technique (Altmann, 1974) was used to record behavioural interactions. This method involves continuously recording the behaviour of, or directed to, a single individual (the focal animal) for a predetermined length of time. This is particularly

appropriate to this study as frequencies, durations and sequences of behaviour are preserved by this means, all of which are necessary for detailed descriptions of social relationships, and the computer method of collecting data used here (see below) meant that all these details could be recorded with great accuracy. The method also allows data to be compared directly across subjects and ages, provided all focal animals (in this case the infants) are observed for equal lengths of time under comparable conditions.

Infants were observed up to the age of 22 weeks, which is approximately when the next set of offspring are due to be born. Infants were watched at 4 week intervals apart from the first 6 weeks when they were watched fortnightly since developmental changes occur fastest at this time. Infants were therefore observed at 2, 4, 6, 10, 14, 18 and 22 weeks of age. Watches at shorter intervals were not possible partly as data was collected from infants from three families at a time, and partly because in the intervening weeks other watches for another project were being carried out.

At each watching age each infant was observed for four one and a half hour sessions, giving a total of six hours of observation at each age. Two of the sessions were begun between 9 and 9.30 am, and two between 12 and 12.30 pm. Pilot observation sessions had previously shown that rates of performance and durations of behaviours did not substantially decrease in variability if individual observation sessions were longer than $1\frac{1}{2}$ hours, but that they increased in variability if fewer than four observations sessions per week were carried out. An acceptably low variability was considered to be a five percent or less change in mean duration or frequency (i.e. number per unit time) of a behaviour with extension of the observation session. A computer program which monitored mean frequencies and durations while

the session was in progress was used for this.

b) Recording.

Recording of data during observation sessions was carried out using an Apple II microcomputer with 48 K of random access memory (RAM) to store data whilst in operation, the Apple 3.2 plus version disc operating system, autostart ROM (read only memory), and printer and disc drive interface cards (manufactured by Apple Computer Inc., Cupertino, California). The computer also contained an Apple Clock, a plug-in printed circuit card with ROM and battery adding real time and date operations for intervals down to one millisecond (Mountain Hardware Inc., Scotts Valley, California). Peripheral equipment used in conjunction with the computer included an Apple Disk II floppy disc drive, Verbatim minidisks for use with the drive (Verbatim Corporation, Sunnyvale, California), a television monitor, and an Axiom EX-801 microprinter (Axiom Corporation, Glendale, California).

The computer was programmed in the Apple II version of BASIC such that each time a key was depressed, the identity of the key and the time that it was pressed were stored in the computer's memory. By assigning a different behaviour to each key a large number of interactions could be easily and accurately recorded. At the end of each observation session this data was transferred onto a disc for storage. In this form it was readily accessible for analysis using other computer programs at a later date. A hard copy was also made of the data from each observation session using the paper printer.

Table 3.2 shows which keys were assigned to the behaviours listed in table 3.1. Where durations were required for non-mutually exclusive behaviours, such as grooming and playing, two keys were needed, one to indicate the beginning and one the end of the behaviour. For

Table 3.2

Designation of computer keys for recording of behaviours.

NON-BEHAVIOUR KEYS

! End program

* Terminal stop code

CAREGIVER IDENTITY KEYS

1 Start father

2 Stop father

3 Start mother

4 Stop mother

5 Start sibling 1

6 Stop sibling 1

7 Start sibling 2

8 Stop sibling 2

9 Start twin

0 Stop twin

BEHAVIOUR KEYS

= Threat/attack

H Off

- Fails to rub off

J Infant gets off

T Successful food-steal

K Caregiver restricts

Y Unsuccessful food-steal

; Rub-off

U Caregiver groom, start

Z Play, start

I Caregiver groom, stop

X Play, stop

O Infant groom, start

C Infant approaches

P Infant groom, stop

V Infant leaves

A Infant is picked up

B Caregiver approaches

S Infant avoids carry

N Caregiver leaves

D Infant gets on

M Contact¹

G Rejection

. Tantrum

/ Ignore

\$ Picks up infant sibling successfully

% Picks up infant sibling unsuccessfully

(Rubs off infant sibling successfully

) Rubs off infant sibling unsuccessfully

Q Caregiver interrupts infant successfully

W Caregiver interrupts infant unsuccessfully

E Infant interrupts caregiver successfully

R Infant interrupts caregiver unsuccessfully

1 'M' without caregiver identity keys around it = Huddle.

mutually exclusive behaviours, durations could be obtained by taking the start of one behaviour as signifying the end of the previous one.

Two non-behaviour key codes were also required, one to mark the end of the session for the analysis programs, and one which functioned to stop the recording part of the program running and allow the data to be transferred to a disc. The former (the 'terminal stop code') was used by the analysis programs in calculating durations of behaviours which were still continuing when the session ended. For example, if the session ended while the infant was in a family huddle, the length of that bout of huddling was measured from the start of the huddle (key M) to the terminal stop code (key *), rather than to the start of the next mutually exclusive behaviour state.

The project required that the identity of the caregiver involved in each interaction with the infant was also recorded. This was accomplished by means of the computer's numeral keys, 1 to 9 and 0. Each caregiver had a 'start' and a 'stop' key assigned to it. At the start of each interaction the start key for the appropriate caregiver was depressed, and the stop key was used when the infant was no longer near enough to interact with that caregiver. If a second caregiver approached while behaviours were being recorded for the first caregiver, interactions could be 'nested' by inserting the second caregiver's start and stop codes around the behaviours it performed with the infant. The analysis programs could only cope with one level of 'nesting' but this was adequate for the present study. The caregiver start and stop keys are also shown in table 3.2.

A small proportion of the total data could not be analysed as it was either lost during storage onto disc due to malfunctioning of the computer's error messages, or was not recorded for unavoidable reasons such as illness. Data lost from Part I consisted of that for

infant number 2 at 10 weeks, number 3 and 2 weeks, number 5 at 14 weeks and number 7 at 6 weeks. No data was lost from Part II.

3.3) ANALYSIS

a) Data processing.

The data taken during each watch was analysed from disc by a program which gave the frequencies and durations of all the behaviours occurring during that watch, and gave them separately according to which caregiver was involved. The results for each of the four watches at each age were added together to give totals representing six hours of observation. Each infant therefore has a set of results for behaviours occurring with each caregiver over a total period of six hours at each watching age.

Means and standard errors were taken of the results for the nine infants of Part I and of the eight infants of Part II and are presented in chapters 4 and 6 respectively. Part II was planned to have nine infants comparable to the nine of Part I, but one set of offspring died (see chapter 2) and as it was not possible to wait another 10 months for another set with older siblings of appropriate age, Part II as a result had only eight infants. In Part I, infant number 2 had only one older sibling and infant number 8 did not have a twin, therefore data for behaviours occurring with sibling 2's and twins in Part I are means of eight sets of data rather than nine. Similarly in Part II, infant number 2 had only one sibling so results for sibling 2's in Part II are means of seven rather than eight individuals. Where data is missing (see section 3.2)) the means are taken from the data from the remaining infants.

Within Part I, results of interactions with different

caregivers are compared using two-tailed randomization tests, as this is the most powerful nonparametric test for paired data, and Spearman rank order correlation coefficients. Where the groups to be compared are of unequal size and the data are not paired (as in comparing frequencies or durations of behaviours performed with different sex older siblings, or in comparing the results of Part II with those of Part I) two-tailed Mann-Whitney U tests are used. Details of these tests can be found in Siegel (1956).

In the description of results in later chapters, statements such as "play develops from 4 weeks" are not meant to imply that the behaviour does not occur before 4 weeks, but only that it was not seen to occur during the previous watching age observations. That is, ages considered to be limits for the performance of behaviours are taken from those ages at which observations were made only.

b) Consequence analysis.

This analysis, which appears in section 4.6) was not done by computer but by hand from the paper printouts of the original data collected during observation sessions for Part I. The printouts list each key pressed along with the exact time (to the nearest millisecond) at which it was pressed. The analysis involved checking through all printouts and for each specified behaviour noting which behaviours followed it within 30 seconds (reasons for this are given in section 4.6)). Results for each of the four watches done on each infant at different ages were summed, and means and standard errors taken over infants at each age.

The methods used for the preliminary drugs tests are given in chapter 5. Details of the subjects used in Parts I and II are given in chapter 2.

c) Use of derived measures.

In this study infant-caregiver relationships are described using both absolute and derived measures of interaction. Derived measures use the relationship between two or more absolute measures to answer questions that are different from or more meaningful than those answered by single absolute measures. Single measures can be combined in various ways, and so to facilitate comparisons the derived measures used here are similar to those used by others, e.g. Ingram (1975a), Hinde & Spencer-Booth (1967).

Hinde and Herrmann (1977) have shown that their derived measures are at least as useful as the absolute measures from which they were composed for describing persistent inter-individual variations in mother-infant relationships.

Derived measures used in this study are:

1. Percentage of total time on spent on each caregiver.

$$\text{i.e. } \frac{\text{time on caregiver n}}{\text{total time carried}} \times 100$$

2. Proportion of time with devoted to play.

$$\text{i.e. } \frac{\text{time playing with caregiver n}}{\text{time with caregiver n}}$$

3. Proportion of caregiver's attempts to pick up infant which are avoided.

$$\text{i.e. } \frac{\text{frequency of infant avoids carry by caregiver n}}{\text{frequency of infant avoids carry by caregiver n} + \text{frequency of caregiver n picks up infant}}$$

4. Relative frequency of rejections (R.F.R.).

$$\text{i.e. } \frac{\text{number of rejections by caregiver n}}{\text{number of rejections by caregiver n} + \text{number of times infant gets on and is picked up by caregiver n}}$$

5. Percentage rub-off success.

$$\text{i.e. } \frac{\text{number of rub-offs by caregiver n}}{\text{number of rub-offs by caregiver n} + \text{number of times caregiver n fails to rub off}} \times 100$$

6. Percentage of tantrums with caregiver.

$$\text{i.e. } \frac{\text{frequency of tantrums with caregiver n}}{\text{total frequency of tantrums}} \times 100$$

7. Percentage success at food-stealing.

$$\text{i.e. } \frac{\text{number of successful food-steals from caregiver n}}{\text{number of successful} + \text{unsuccessful food-steals from caregiver n}} \times 100$$

8. Prox.CG - Prox.I.

i.e. Mean bout length of episodes of proximity terminated by the caregiver minus mean bout length of episodes of proximity terminated by the infant. A bout of proximity is measured from an approach to a leaving between the two animals.

9. Social competence score.

See section 4.8. for details.

10. %AP.I - %LV.I.

11. %ONS.I - %OFFS.I.

%AP.I - %LV.I and %ONS.I - %OFFS.I are examples of a type of measure devised by Hinde and called a responsibility index (e.g. Hinde & Atkinson, 1970; Hinde & Proctor, 1977; Hinde & Spencer-Booth, 1967; Hinde & White, 1974). %AP.I - %LV.I is an index of the infant's relative responsibility for proximity maintenance at any one time. It is calculated as the difference between the percentage of all approaches by the infant and a caregiver to each other which are made by the infant (%AP.I), and the percentage of all the leavings between them which are due to the infant (%LV.I). Similarly, %ONS.I - %OFFS.I as used here is an index of the infant's relative responsibility for time on, being the percentage of initiations of bouts of time on due to the infant minus the

percentage of terminations of bouts of time on due to the infant.

The indices are only useful as indicators of responsibility if interactions are not mediated by cues over a distance. This assumption was made since these cues, even if present, cannot be accurately and reliably observed and measured.

Values of the indices range from + 100 to - 100. A positive value indicates that the infant is playing a relatively larger role in the maintenance of proximity or time on than the other partner. A negative value indicates that the primary responsibility for maintaining the interaction is with the other individual. A zero value indicates that both partners are playing equal roles in maintaining the interaction. The advantage of these indices is that they are largely independent of differences in activity levels between the two partners, provided the frequencies of interaction are sufficiently high. If frequencies for one or both partners are low, the interpretation of small values of the measure becomes ambiguous (Ingram, 1975a) and absolute values of the index are exaggerated (Berman, 1978a). However, even when frequencies are low the sign (positive or negative) of the index will not be affected, so it is possible to tell which partner is playing the relatively greater role in maintaining the interaction, though it is not always clear how much greater this is.

In this study, frequencies for approaches, leavings, 'ons' and 'offs' between infants and specific caregivers were generally low and so the indices were only used for the total frequencies of interactions with all caregivers in Parts I and II (as opposed to having separate indices for interactions by infants with each different caregiver) and for the results of the drug tests where frequencies tended to be higher (see chapter 5). Despite this, the indices are a useful and descriptive way of giving an immediate picture of the situation between interacting individuals.

CHAPTER 4 - Undisturbed Infant-Caregiver Relationships

4.1) INTRODUCTION

This chapter presents the results from Part I of the study and describes the form and development of social interactions between infant marmosets and their parents, older siblings and twins from the age of 2 weeks to 22 weeks. The situation in which the data were collected was uncomplicated by experimental procedures and without interference by handling of the animals except for routine weighing of the infants each fortnight up to the age of 8 weeks, hence this was the "undisturbed" situation.

The data were collected as set out in chapter 3. Definitions of all behavioural categories mentioned in this chapter are also given in chapter 3. Unless otherwise stated, data is presented as the mean score (of frequency or duration) for the nine infant subjects at each watching age. Since a total of six hours of observation was carried out on each infant at each age, the data are therefore mean scores per six hours of observation time. Where data were lost (see chapter 3) the results are the mean of eight subjects. Unless otherwise stated, the significance of data refers to the results of two-tailed randomization tests with a 5% significance level (Siegel, 1956). This test was chosen as the most powerful non-parametric paired test appropriate to the data.

The results are given below grouped into three sections for clarity. The first section deals with the behavioural states, that is, time with, on, grooming, playing, in contact, huddling and off. The second section deals with the events associated with the initiation and termination of these states. The third section deals with the remaining events which were recorded. Because of the difficulty of interpreting

data relating to one behaviour without reference to data on other behaviours, the three results sections below contain a minimum of analysis and are designed simply to present and describe the data. The results are interpreted and compared in the succeeding section (4.5) and analysed further in terms of consequences of behaviour, sex and family differences in further sections. The last section (4.9) consists of a general discussion of the data and suggests a model to explain marmoset infant social development.

4.2) RESULTS 1 - Course of development of behaviour states.

a) Time with

Figure 4.1 shows the mean percentage of time that infants spend with each caregiver. Excluding the twin, infants spend smaller amounts of time with their caregivers as they grow older. This decline is more rapid with respect to siblings than parents, and with respect to fathers than mothers. Table 4.1 confirms that infants spend significantly more time with fathers than with siblings at 2, 4 and 6 weeks and significantly more time with mothers than with siblings at 4, 6, 10 and 14 weeks. They spend significantly more time with mothers than with fathers at 10 and 14 weeks, and with mothers than twins at 4 weeks. However, significantly more time is spent with twins than with fathers at 10, 14, 18 and 22 weeks, and with twins than siblings at 6, 10, 14, 18 and 22 weeks.

At 2 weeks infants do not interact with each other but spend most of their time close to each other as a result of being carried by the same caregiver. Precise figures are not available as data on how many infants each caregiver was carrying at a time were not collected. Time spent with the twin therefore also declines with age but more

Figure 4.1

Mean percentage of time infants spend with each caregiver from 2 to 22 weeks of age. Each vertical line denotes one standard error.

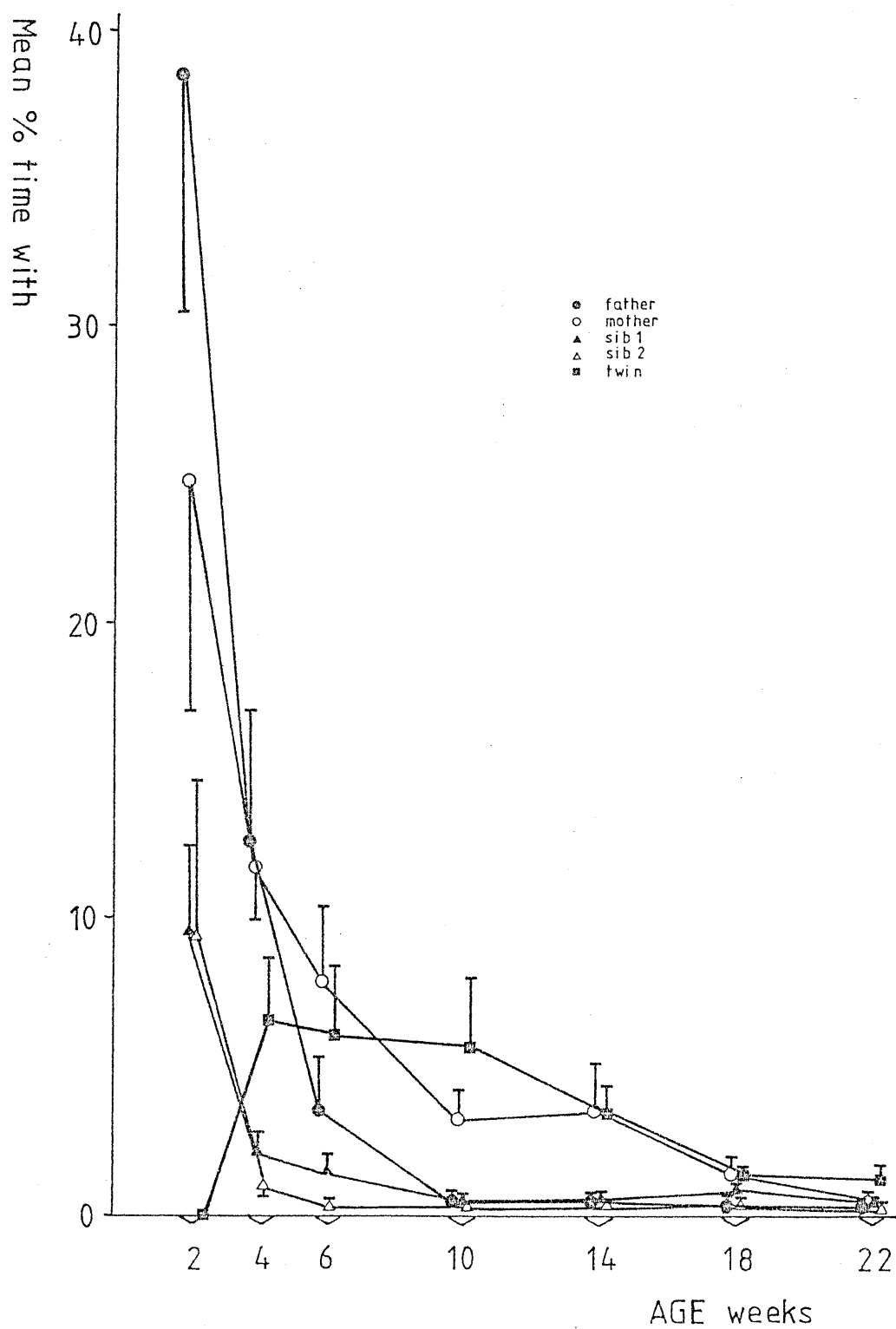


Table 4.1

Differences in the percentage of time infants spent with different caregivers. Two-tailed randomization tests with a 5% significance level.
 - not applicable. ns not significant. * significant difference in time spent with the two caregivers. > more time spent with first caregiver in lefthand column. < more time spent with second caregiver.

CAREGIVERS	AGE/weeks						
	2	4	6	10	14	18	22
Mother vs father	ns	ns	ns	* >	* >	ns	ns
Mother vs sib 1	ns	* >	* >	* >	* >	ns	ns
Mother vs sib 2	ns	* >	* >	* >	* >	ns	ns
Twin vs mother	-	* <	ns	ns	ns	ns	ns
Twin vs father	-	ns	ns	* >	* >	* >	* >
Twin vs sib 1	-	ns	ns	ns	ns	ns	* >
Twin vs sib 2	-	ns	* >	* >	* >	* >	ns
Father vs sib 1	* >	* >	ns	ns	ns	ns	ns
Father vs sib 2	* >	* >	* >	ns	ns	ns	ns

slowly than for other caregivers, and twins are most important in terms of time with from 10 weeks onwards, though the amount of time spent with the twin is not significantly greater than that spent with the mother.

b) Time on

Figures 4.2 and 4.3 show the mean percentage of time infants spend on each caregiver and the mean time on each caregiver as a percentage of the total time on all caregivers at each age. As for time with, time on caregivers decreases with age and infants are rarely carried from 10 weeks onwards (see figure 4.2). Siblings carry less than parents and twins do not carry at all. Although fathers do by far the most carrying at 2 weeks, an increasing proportion of the time spent on is spent on the mother (see figure 4.3) and by 14 weeks she alone carries the infant. Significant differences between the proportion of time infants spend on each caregiver are shown in table 4.2. Fathers carry infants for a significantly higher proportion of the time than sibling 1 at 2, 4 and 10 weeks, and than sibling 2 at 2, 4 and 6 weeks, though the difference between time on fathers and on mothers is not significant at 2 or 4 weeks.

Mothers become increasingly important as carriers and carry infants significantly more than both siblings at all ages except 2 weeks, and more than fathers at all ages except 2 and 4 weeks.

The mean bout length of episodes of time on gets shorter as infants get older (see table 4.3), so as infants get older they are spending less time on, and the time on is divided up into shorter bouts.

Figure 4.2

Mean percentage of time infants spend on different caregivers at each age. Conventions as in figure 4.1.

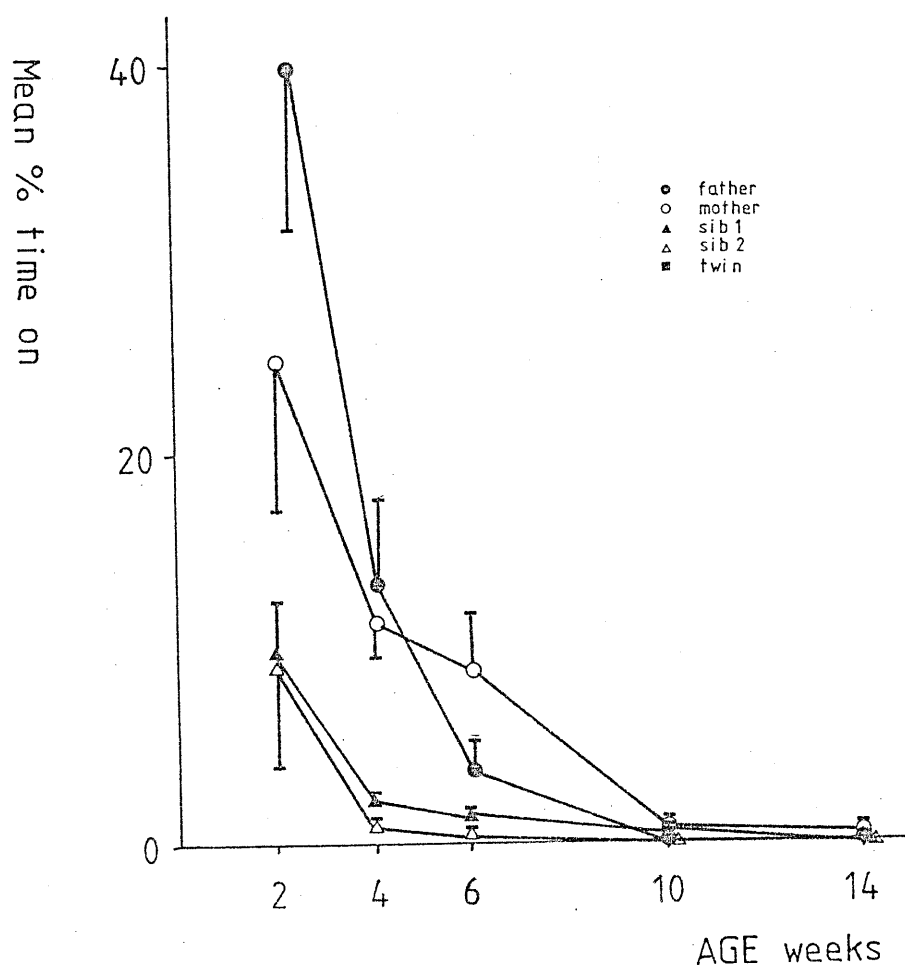


Figure 4.3

Mean amount of time infants spend on each caregiver as a percentage of the total time spent on caregivers at that age. Conventions as in figure 4.1.

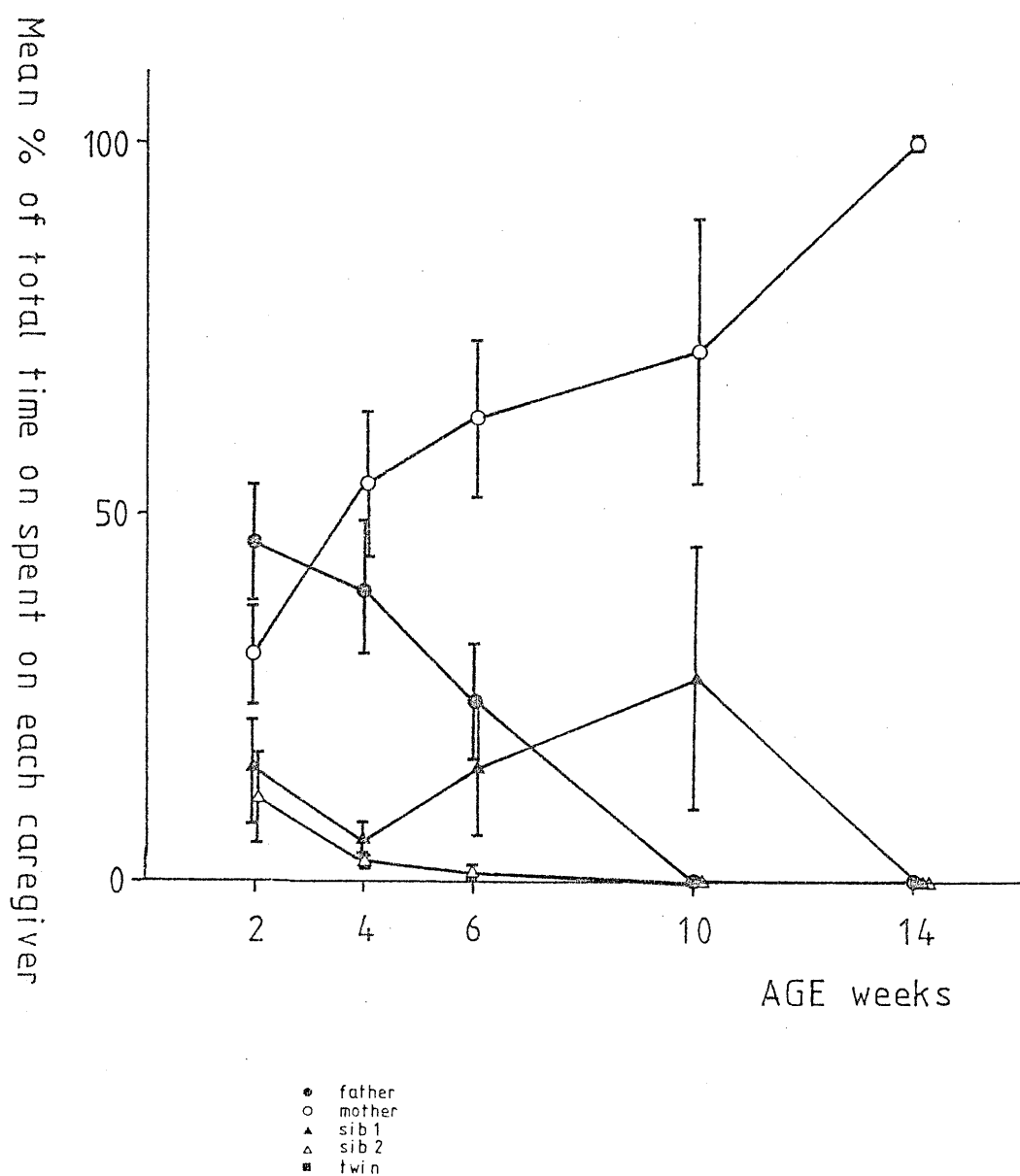


Table 4.2

Differences in the relative importance of different caregivers as carriers. Randomization tests between time on caregivers as percentage of total time on all caregivers, for different pairs of caregivers. Conventions as in table 4.1.

CAREGIVERS	AGE/weeks				
	2	4	6	10	14
Father vs sib 1	* >	* >	ns	* <	ns
Father vs sib 2	* >	* >	* >	ns	ns
Mother vs sib 1	ns	* >	* >	* >	* >
Mother vs sib 2	ns	* >	* >	* >	* >
Father vs mother	ns	ns	* >	* >	* >

Table 4.3

Mean bout length of time on different caregivers. Mean time on in seconds divided by mean frequency of bouts of time on with each caregiver at each age.

CAREGIVER	AGE/weeks				
	2	4	6	10	14
Father	1319.49	464.94	236.73	-	-
Mother	907.20	491.74	484.99	167.49	44.70
Sib 1	572.66	179.12	96.52	17.48	-
Sib 2	700.84	117.02	21.54	-	-

c) Grooming

Figure 4.4 shows the mean percentage of time caregivers spend grooming the infant, while figure 4.5 shows the mean percentage of time infants spend grooming their caregivers.

Infants are groomed by their caregivers progressively less as they grow older. Fathers on the whole groom most (significantly so at 6 weeks) while twins groom hardly at all. Grooming by siblings varies widely with age and from sibling to sibling.

In contrast, infants tend to increase the amount of time they spend grooming caregivers with age, but concentrate on grooming mothers. This reaches a peak at 10 weeks though mothers are groomed significantly more than other caregivers at 10, 14 and 18 weeks. Twins are groomed hardly at all.

In addition to absolute time spent grooming, fathers generally spend a higher proportion of their time with infants in grooming than do other caregivers. This is significant with respect to mothers at 6 weeks, with respect to sibling 1's at 6 and 22 weeks, with respect to sibling 2's at 14 and 22 weeks and with respect to twins at all ages.

d) Contact with each caregiver and family huddling

Figure 4.6 shows the mean percentage of time spent by infants in contact with each caregiver, and figure 4.7 shows the mean percentage of time spent by infants in family huddles.

Contact with caregivers does not occur at 2 weeks of age, except for a very small amount (0.009%) with twins, as most time is spent on. However from 4 weeks the amount of time in contact increases dramatically, particularly with the twin. Time in contact with fathers and older siblings remains low, not rising above 0.5%. Time in contact with twins is at a peak at 4 weeks but declines slowly to be overtaken

Figure 4.4

Mean percentage of time that infants are groomed by each caregiver at each age. Conventions as in figure 4.1.

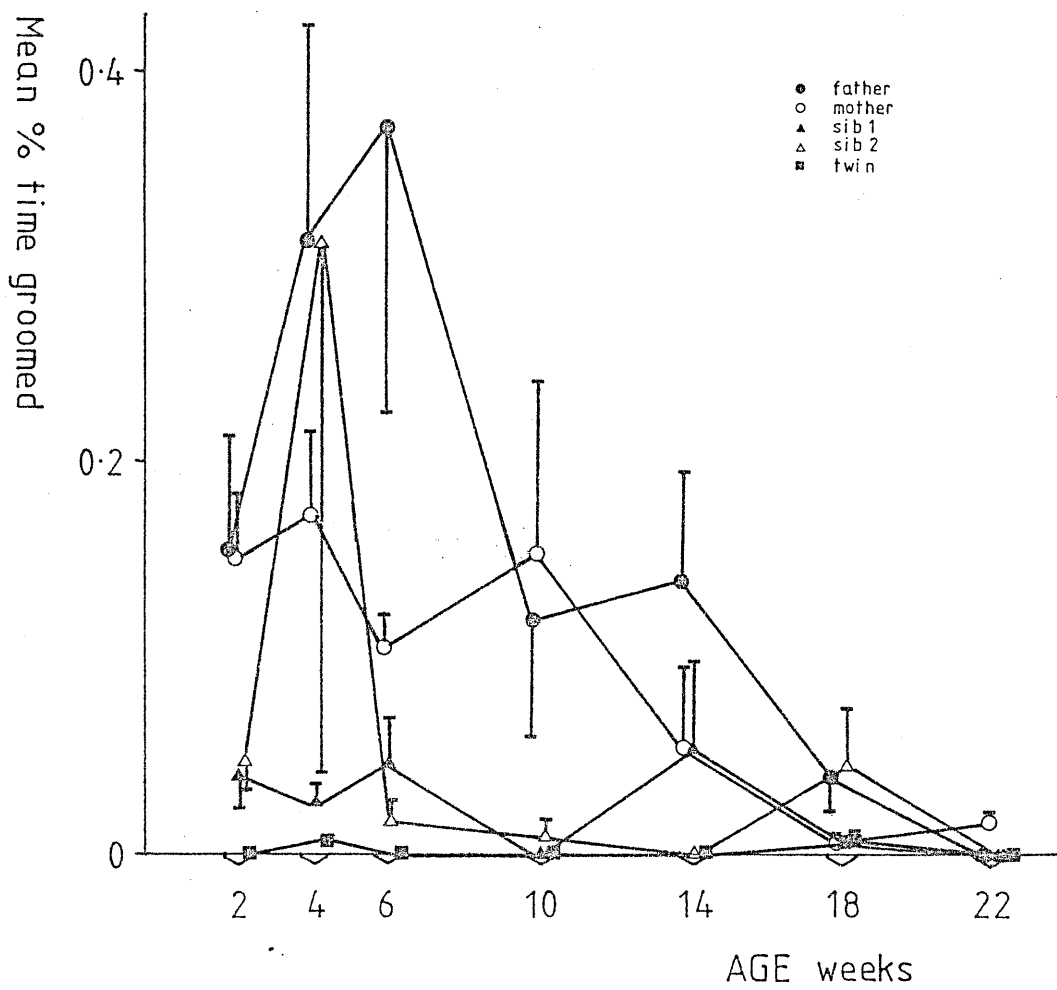


Figure 4.5

Mean percentage of time that caregivers are groomed by infants.

Conventions as in figure 4.1.

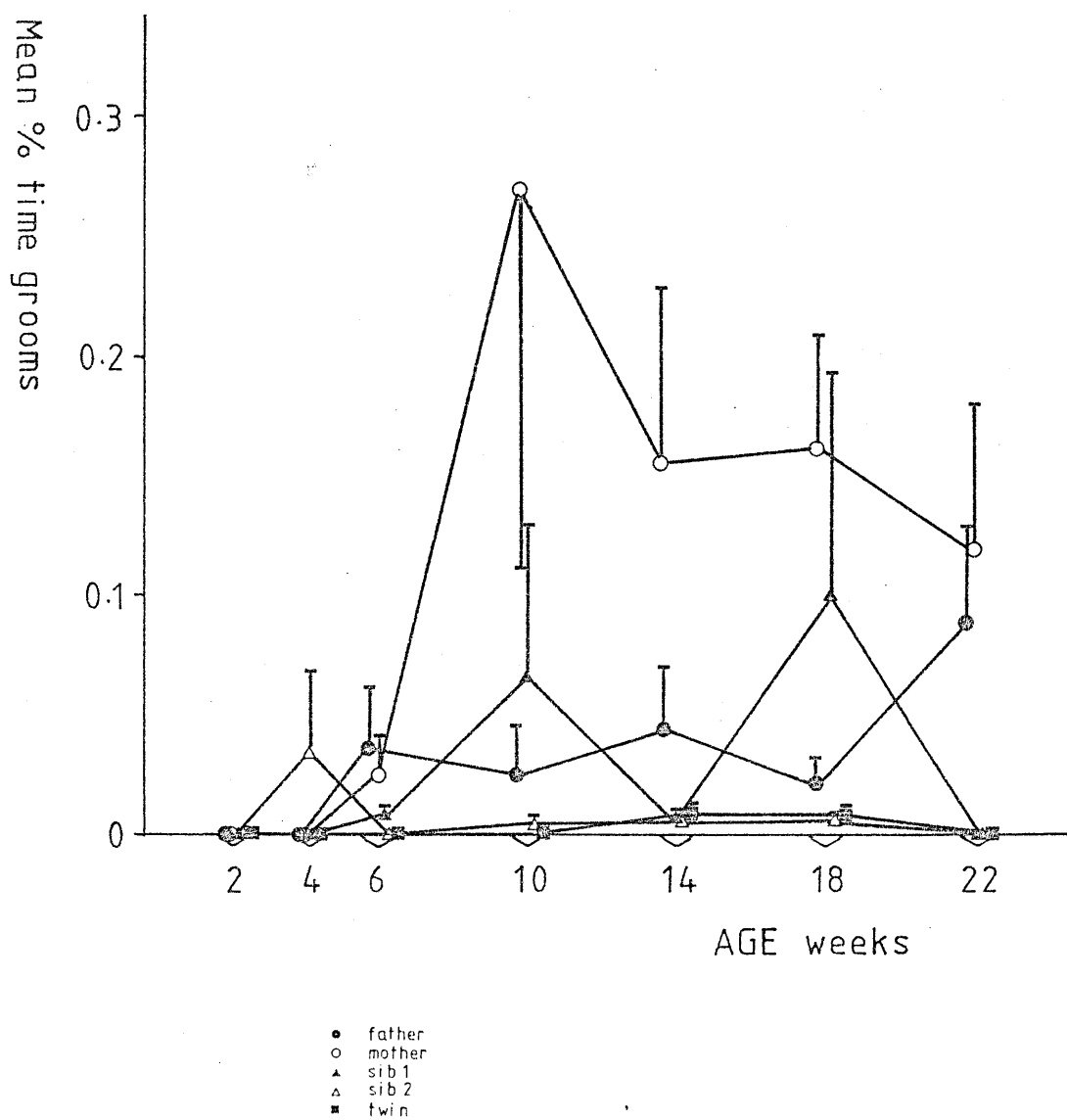
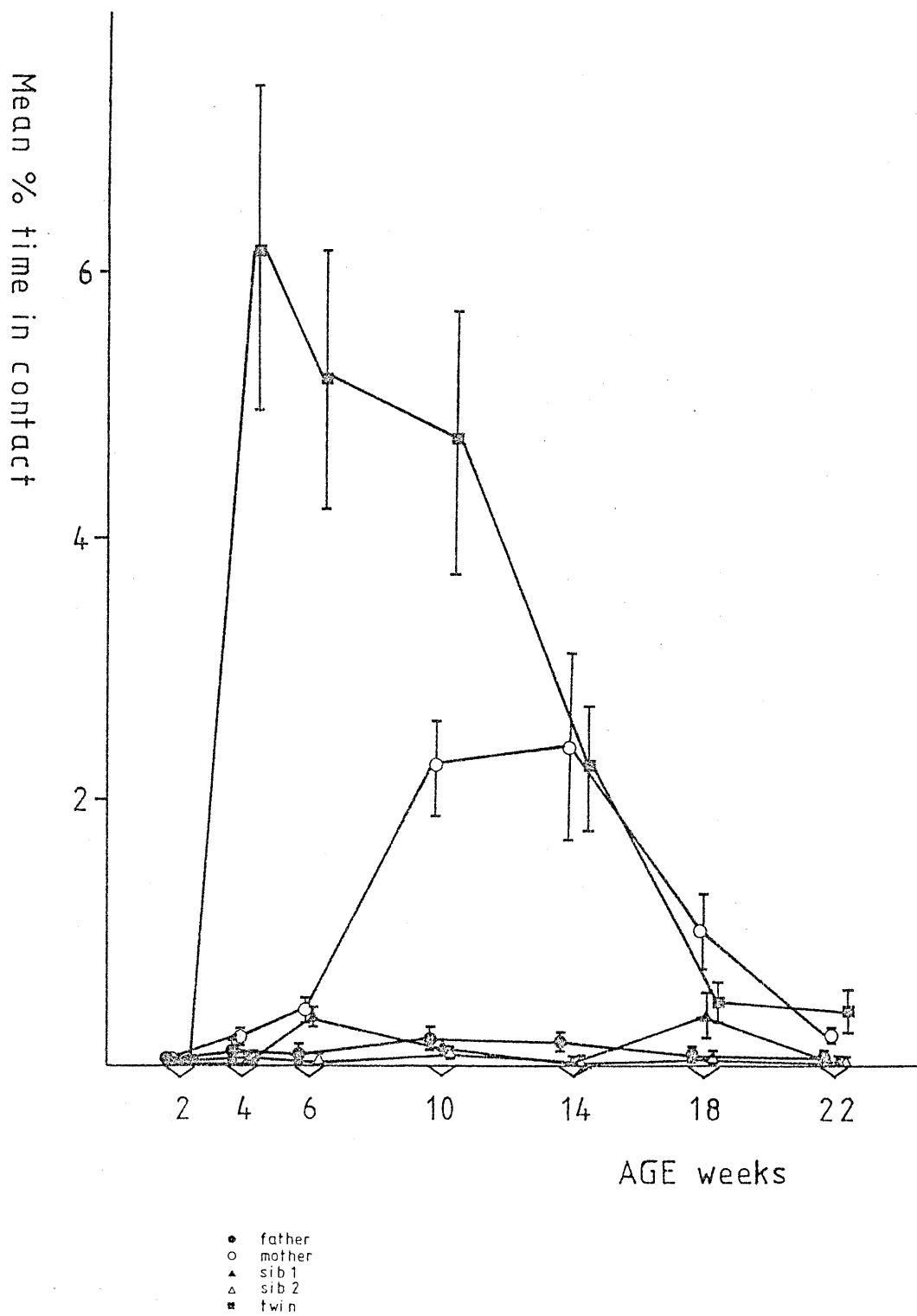


Figure 4.6

Mean percentage of time infants spend in contact with caregivers.

Conventions as in figure 4.1.



by time in contact with mothers, this peaks at about 3% at 14 weeks and declines thereafter.

Of the time with caregivers that is devoted to contact, infants spend a significantly higher proportion of this time in contact with twins than with fathers at 2, 4, 6 and 22 weeks, with twins than mothers at 2, 4 and 6 weeks, and with twins than siblings at all ages except 22 weeks. A significantly higher proportion of time is spent in contact with mothers than with twins at 18 weeks, with mothers than fathers at 10 and 22 weeks, and with mothers than siblings at 10, 14, 18 and 22 weeks (see table 4.4).

Figure 4.7 shows a steady increase in time spent in family huddles with age from a very small amount at 2 weeks (about 0.1%) to a plateau of about 16%. A dip in this trend is apparent at 10 weeks. This was also found by Ingram for "huddling with parents" (Ingram, 1975a). A similar dip occurs in time off at this age, see below.

e) Play

Figure 4.8 shows the mean percentage of time infants spend playing with other caregivers. Play develops from 4 weeks mainly with the infant's twin but also with the siblings. Parents were not observed to play with infants. About 1% of the infant's time is spent playing with its twin from 6 weeks of age onwards, considerably more than play with siblings which reaches a maximum of less than 0.3% for each sibling at 14 weeks of age. Infants spend significantly more time playing with twins than with either sibling at all ages, and significantly more time playing with twins than the total time for both siblings combined at all ages except 18 and 22 weeks.

However, as a proportion of the total time spent with infants, siblings spend most of their time with infants playing (see figure 4.9)

Table 4.4

Differences between caregivers in the proportion of their time with infants that is devoted to contact. Results of randomization tests, conventions as in table 4.1.

CAREGIVERS	AGE/weeks						
	2	4	6	10	14	18	22
Mother vs father	-	ns	ns	* >	ns	ns	* >
Mother vs sib 1	-	ns	ns	* >	* >	* >	* >
Mother vs sib 2	-	ns	ns	* >	* >	* >	* >
Mother vs twin	* <	* <	* <	ns	ns	* >	ns
Twin vs father	* >	* >	* >	ns	ns	ns	* >
Twin vs sib 1	* >	* >	* >	* >	* >	ns	* >
Twin vs sib 2	* >	* >	* >	* >	* >	ns	* >

Figure 4.7

Mean percentage of time infants spend in family huddles. Vertical bars represent one standard error either side of the mean.

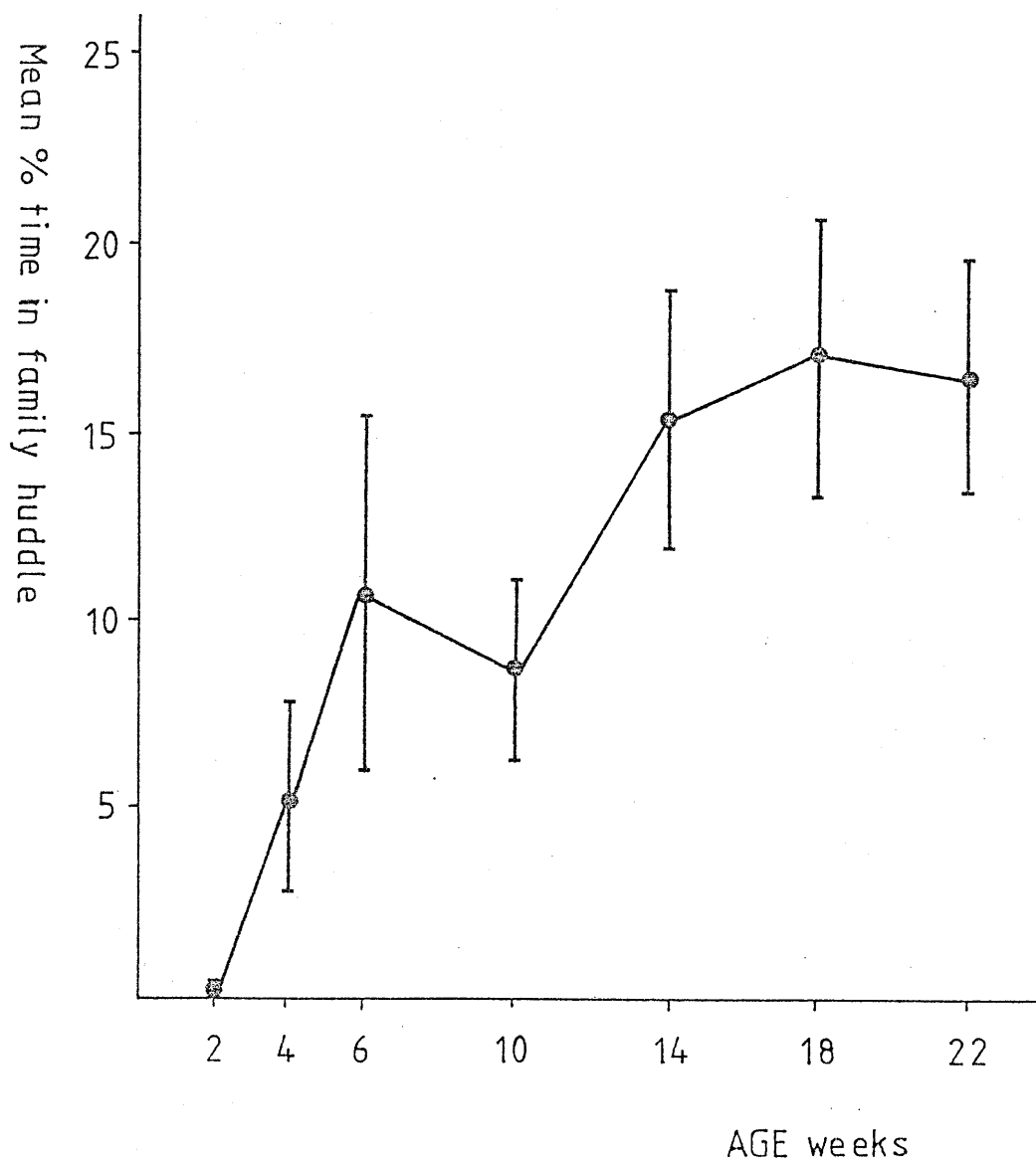


Figure 4.8

Mean percentage of time infants spend playing with caregivers.

Conventions as in figure 4.1.

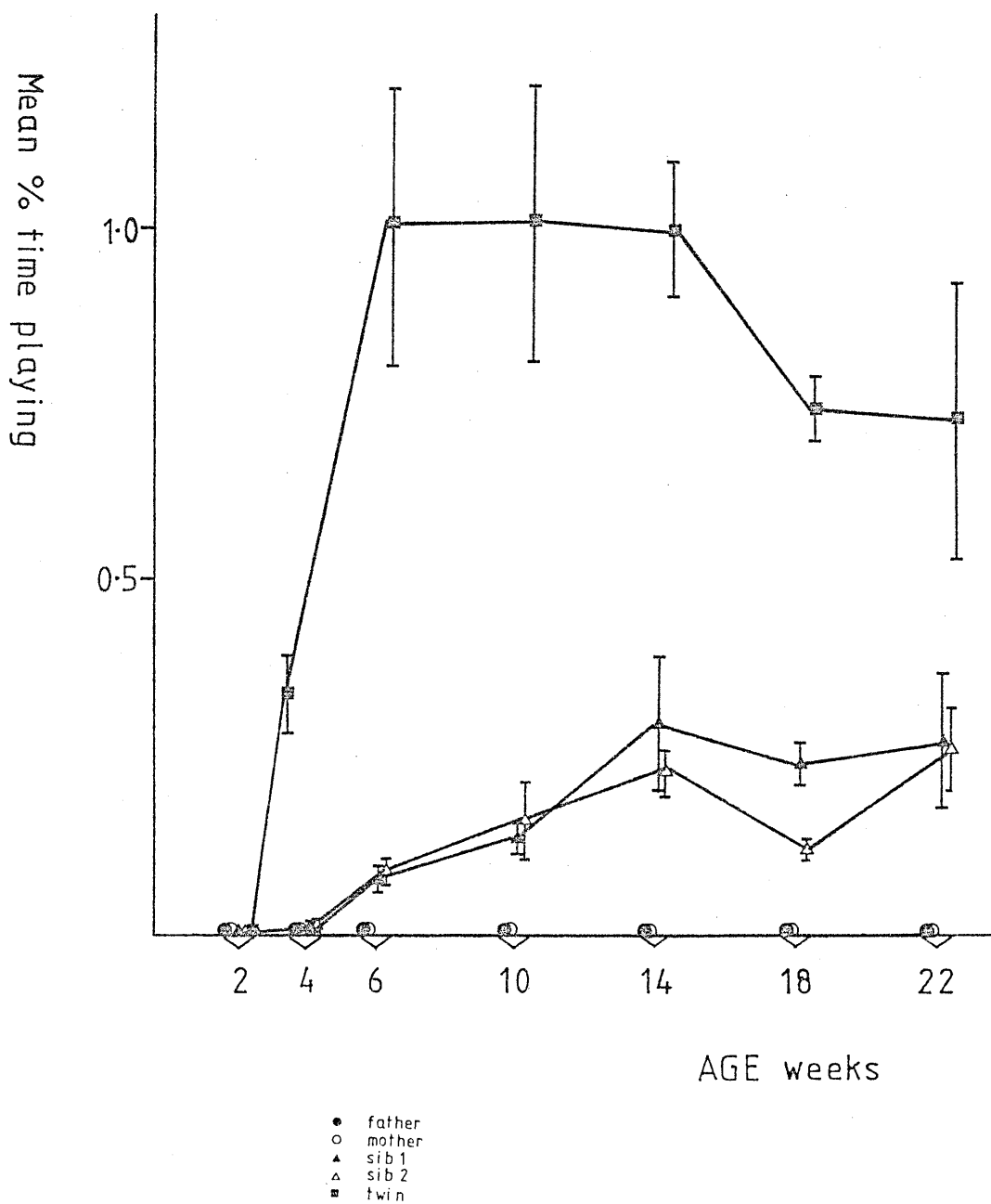
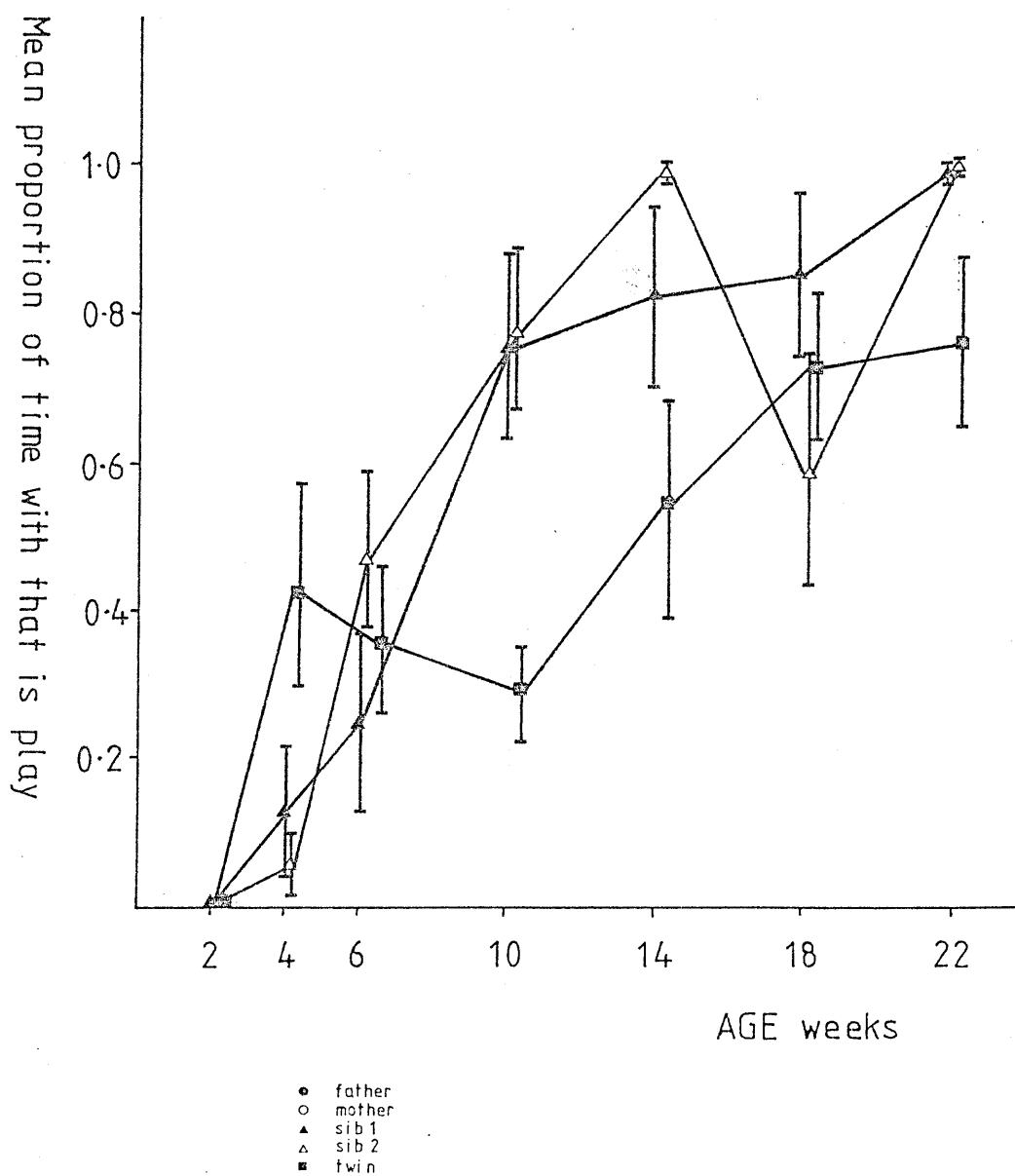


Figure 4.9

Mean proportion of total time spent with infants that is devoted to play by siblings and twins. Conventions as in figure 4.1.



whereas twins spend some of this time in contact (see figure 4.6). The proportion of time spent with the infant devoted to play is significantly higher for sibling 1's than for twins at 22 weeks, and significantly higher for sibling 2's than twins at 10, 14 and 22 weeks.

f) Time off

As can be seen from figure 4.10, time off increases dramatically after 2 weeks of age, the rate of increase slowing after 6 weeks until the maximum of 84% is reached at 22 weeks. The slight drop at 10 weeks (which also occurred in family huddle at 10 weeks) is discussed below.

The changes in the proportion of time spent in the mutually exclusive states of on, off, huddle and contact are shown in figure 4.11. The amount of time on rapidly decreases while off, huddle and contact increase. Off increases most rapidly, while contact decreases again after 10 weeks. This shows that time on is replaced temporally by time in contact which then itself declines as the infant comes to spend most of its time alone and the rest in family huddles.

The dip in mean time in family huddles and in time off at 10 weeks noted above can be seen to be due to the increase in total time spent in contact with specific individuals at this age. Contact therefore increases as time on decreases and is particularly important at 10 weeks of age. A Spearman rank order correlation between total time on and total time in contact from 2 to 14 weeks (on does not occur after this) gives $r_s = -0.3$, $p > 0.5$. Though the correlation is negative it is not significant because other factors are involved. For example play (figure 4.8) is also increasing with age.

Figure 4.10

Mean percentage of time infants spend off and away from caregivers.
Vertical bars represent one standard error either side of the mean.

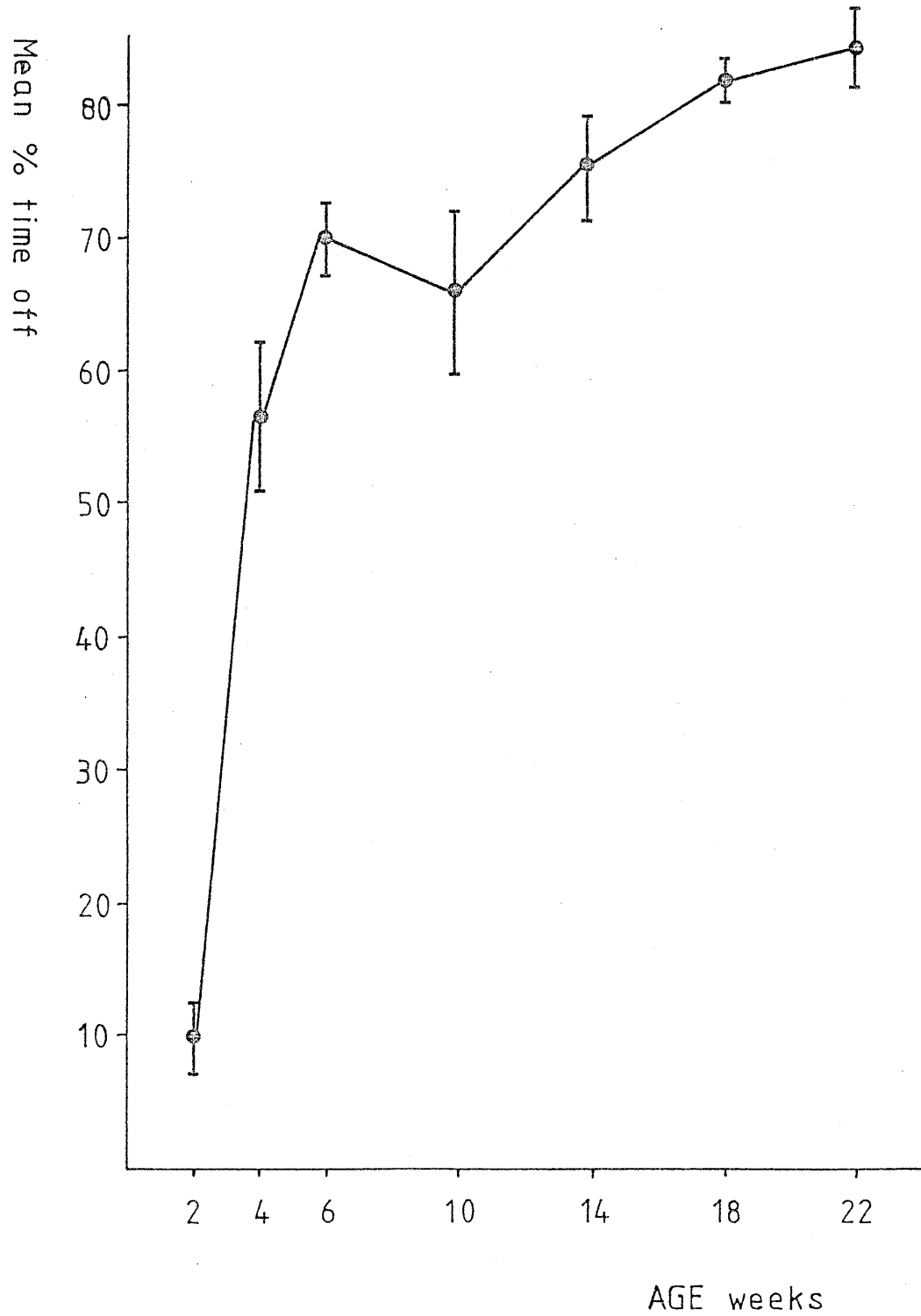
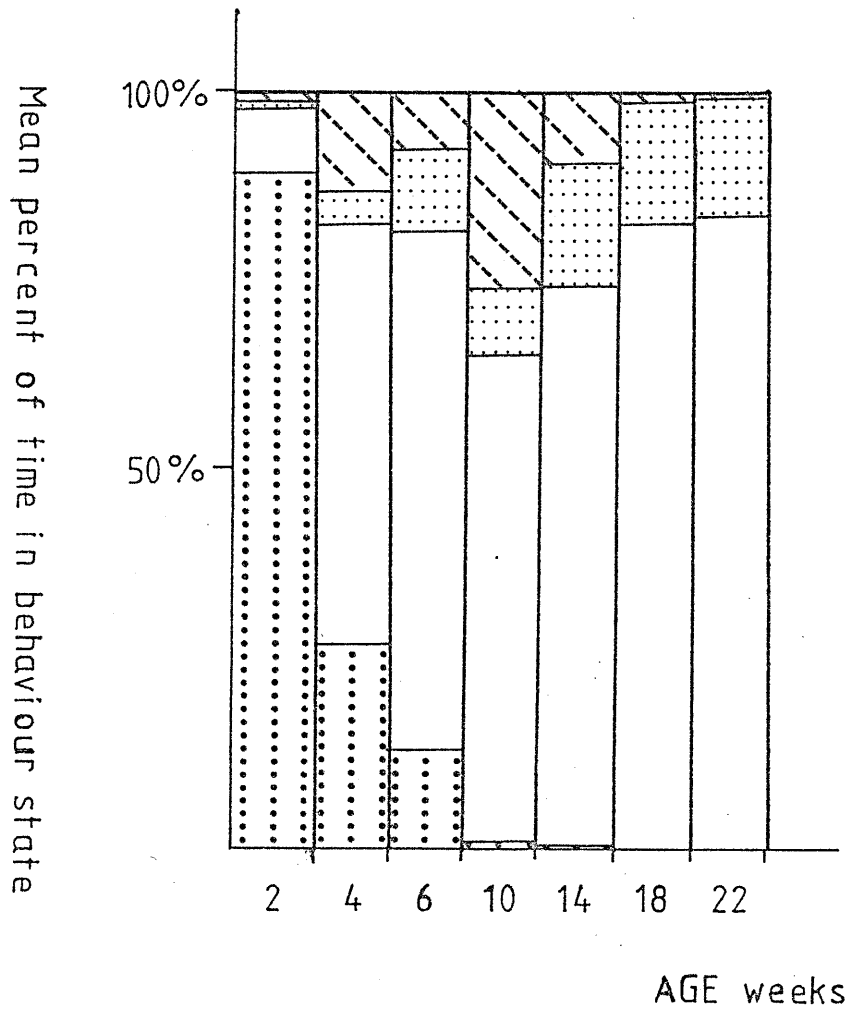
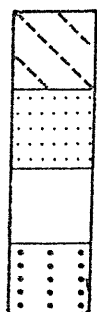


Figure 4.11

Mean percentage of total observation time spent in each mutually exclusive behaviour state: On, off, huddle, contact.



KEY



Contact

Huddle

Off

On

4.3) RESULTS 2 - Patterning of events associated with behaviour states.

a) Approaching and leaving

Figure 4.12 shows mean %AP.I - %LV.I for all caregivers combined, i.e. the index indicates general proximity maintenance by infants to all family members. From a negative score at 2 weeks there is a sharp rise peaking at 6 weeks then dropping off slowly to a lower, though still positive, level at 22 weeks. At most ages the infant is maintaining proximity with its caregivers more than they are with it and this is most apparent at 6 weeks. Only at 2 weeks are the caregivers more responsible than the infant for the maintenance of proximity between them. This compares well with Ingram's (1975a) data on marmosets, and in overall form (i.e. changing from negative to positive values) with work done on rhesus monkeys (Berman, 1978a; Hinde, 1969; Hinde & Spencer-Booth, 1967, though here only mother - infant relations are considered).

Data for individual caregivers cannot be presented as %AP.I - %LV.I scores since mean frequencies of approaching and leaving are mostly less than 20 and the index becomes unreliable if low figures are used (see Hinde & Atkinson, 1970). Instead, data are shown as histograms of mean frequencies of approaching and leaving by infants and by each caregiver (figures 4.13 - 4.17). Where differences in frequencies of approaching or leaving between infant and caregiver are significant, this is shown by an asterisk over the significantly larger score at each age. However it is the changes with age in relative frequencies by caregivers and by infants that is important, rather than the overall size of the differences between them.

i) Fathers (figure 4.13)

Infants initiate an increasing number and proportion of approaches up to 6 and 10 weeks of age respectively. After this, the differences in

Figure 4.12

Maintenance of proximity with all caregivers by infants. Percentage of total approaches made by the infant minus percentage of total leavings made by the infant, means and standard errors for infants at each age.

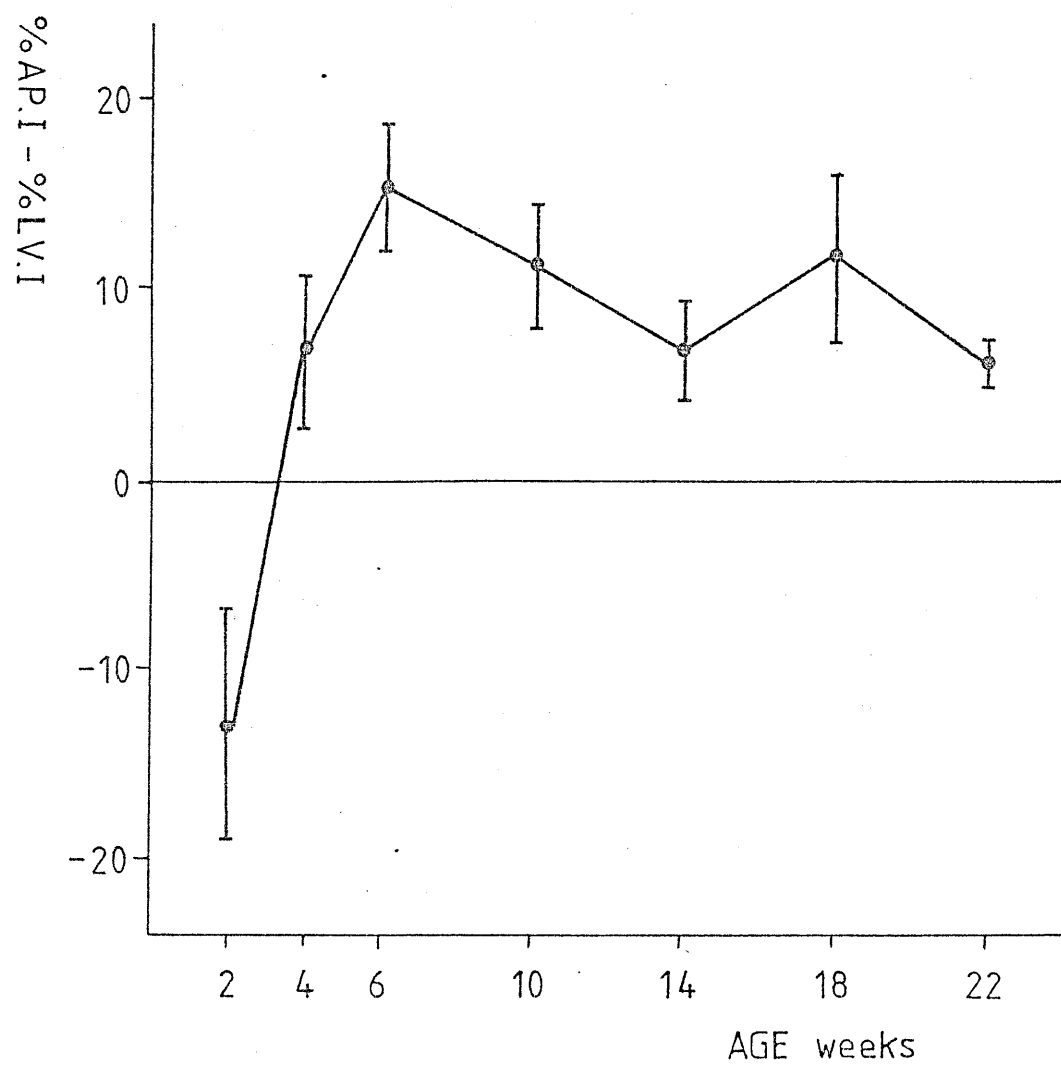
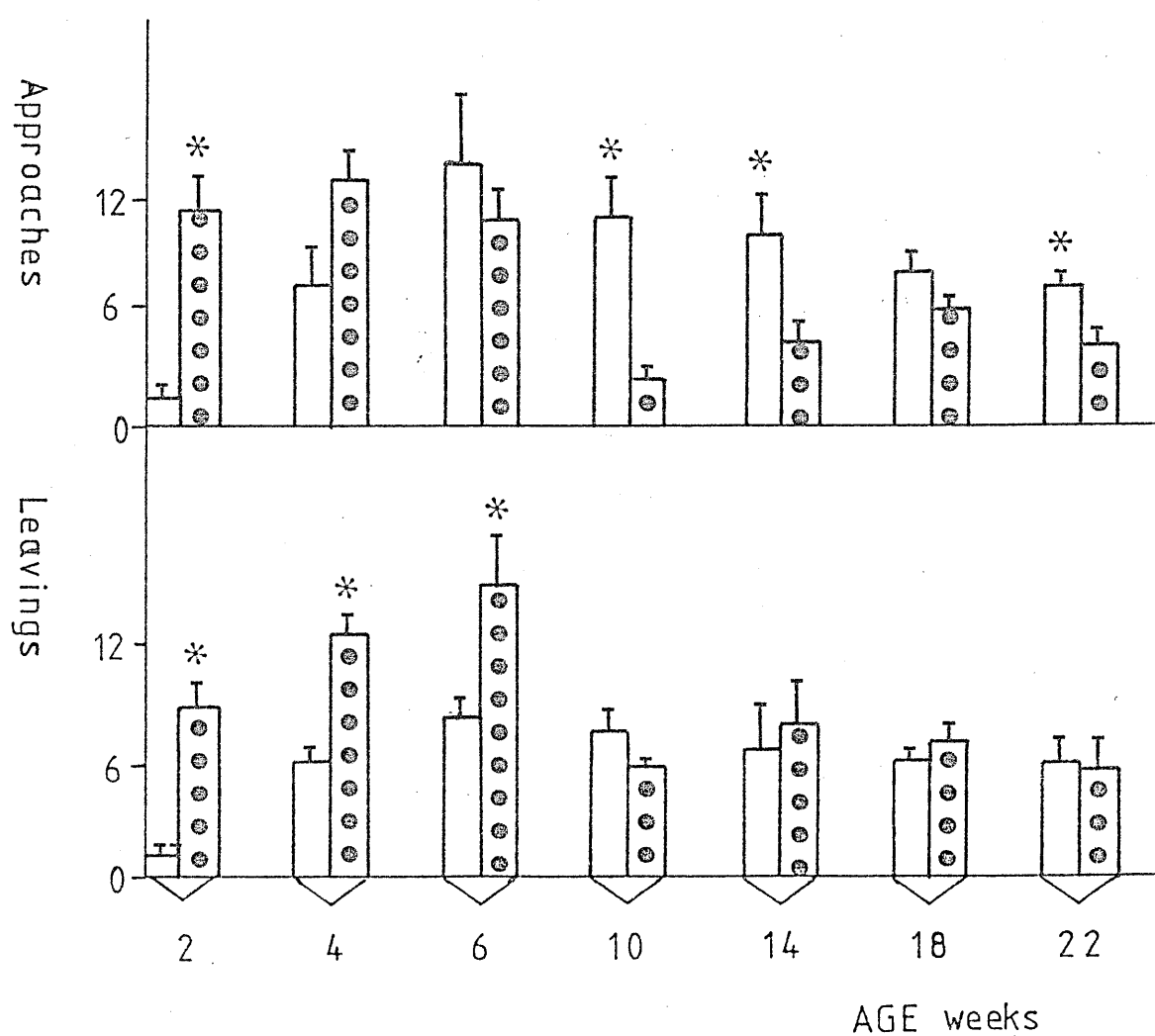


Figure 4.13

Mean frequencies of approaching and leaving between fathers and infants. Vertical bars indicate one standard error.

Asterisks indicate a significant difference between caregiver and infant scores at that age (two-tailed randomization test, $p < 0.05$).

Open bars denote approaches and leavings by infants, dotted bars denote approaches and leavings by caregivers.



approaching between fathers and infants decrease as infants begin to approach less and fathers approach slightly more (fathers approach infants significantly more than infants approach fathers at 2 weeks, and significantly less at 10, 14 and 22 weeks).

Fathers leave significantly more often than infants at 2, 4 and 6 weeks, though subsequently leavings by fathers and by infants are not significantly different. Thus, infants take over responsibility for maintenance of proximity with fathers from fathers at about 4 weeks of age, but their role declines from about 14 weeks as responsibility becomes more evenly divided between them.

ii) Mothers (figure 4.14)

As with fathers, infants initiate an increasing number of approaches to mothers but the proportion of approaches by infants remains high to 22 weeks. Approaches by mothers decrease in frequency rapidly and remain at a low level. (Mothers approach infants significantly more often than infants approach mothers at 2 weeks, and significantly less often from 6 to 22 weeks.)

Infants leave less than mothers (significantly so at 2, 4, 6 and 14 weeks) until 18 weeks when leavings by mothers and infants are about equal. Infants therefore are responsible for proximity with mothers at all ages except 2 weeks when mothers do most approaching and leaving.

iii) Siblings (figures 4.15 and 4.16)

At 2 weeks siblings are approaching infants more than they are leaving them and are responsible for maintaining proximity as infants approach and leave very little. However the situation gradually reverses as infants initiate an increasing proportion of approaches. By 6 to 10 weeks proximity maintenance is mainly due to the infant. From 10 weeks, frequencies of approaching and leaving by siblings and infants are

Figure 4.14

Mean frequencies of approaching and leaving between mothers and infants.
Conventions as in figure 4.13.

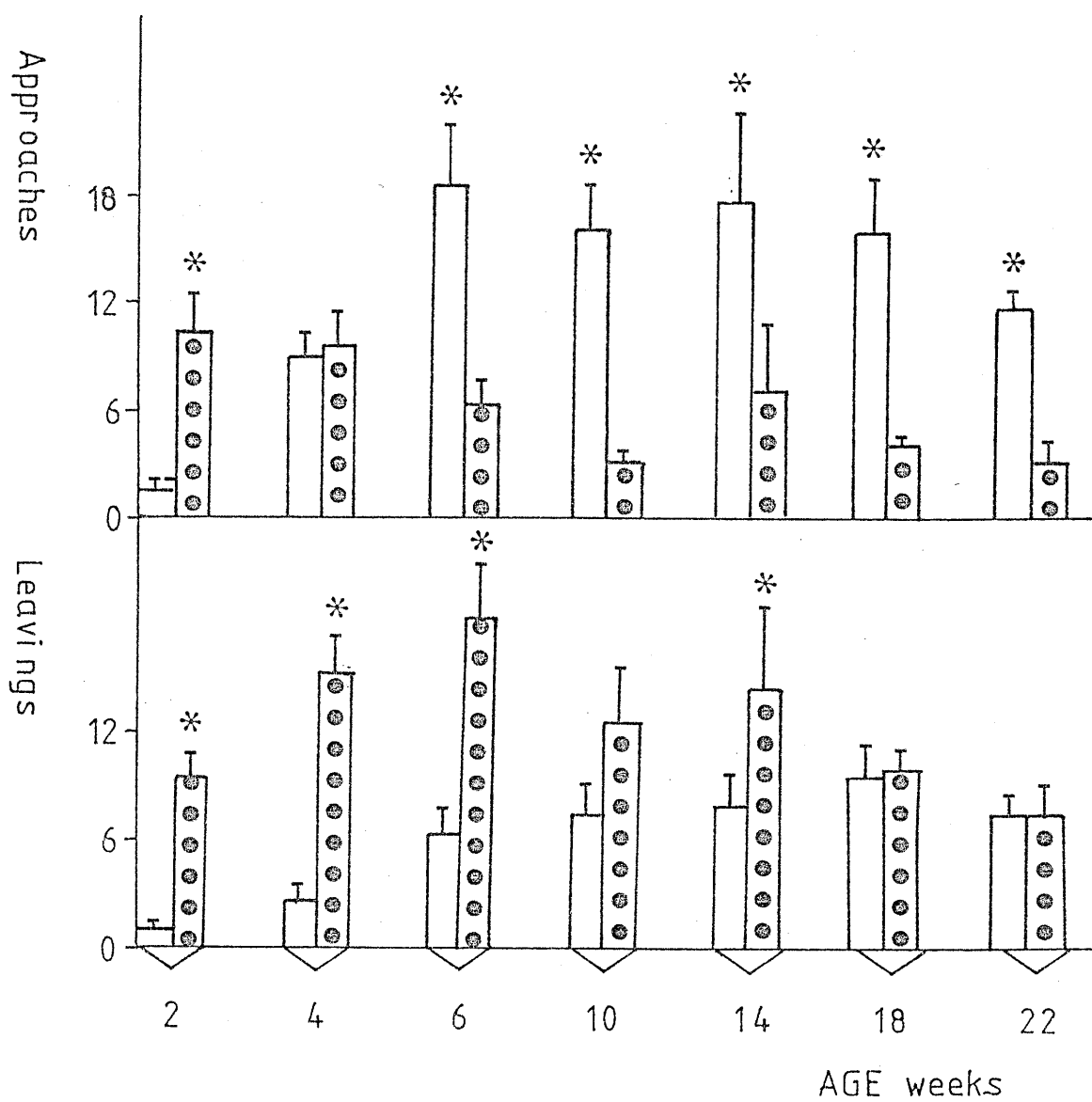


Figure 4.15

Mean frequencies of approaching and leaving between sibling 1's and infants. Conventions as in figure 4.13.

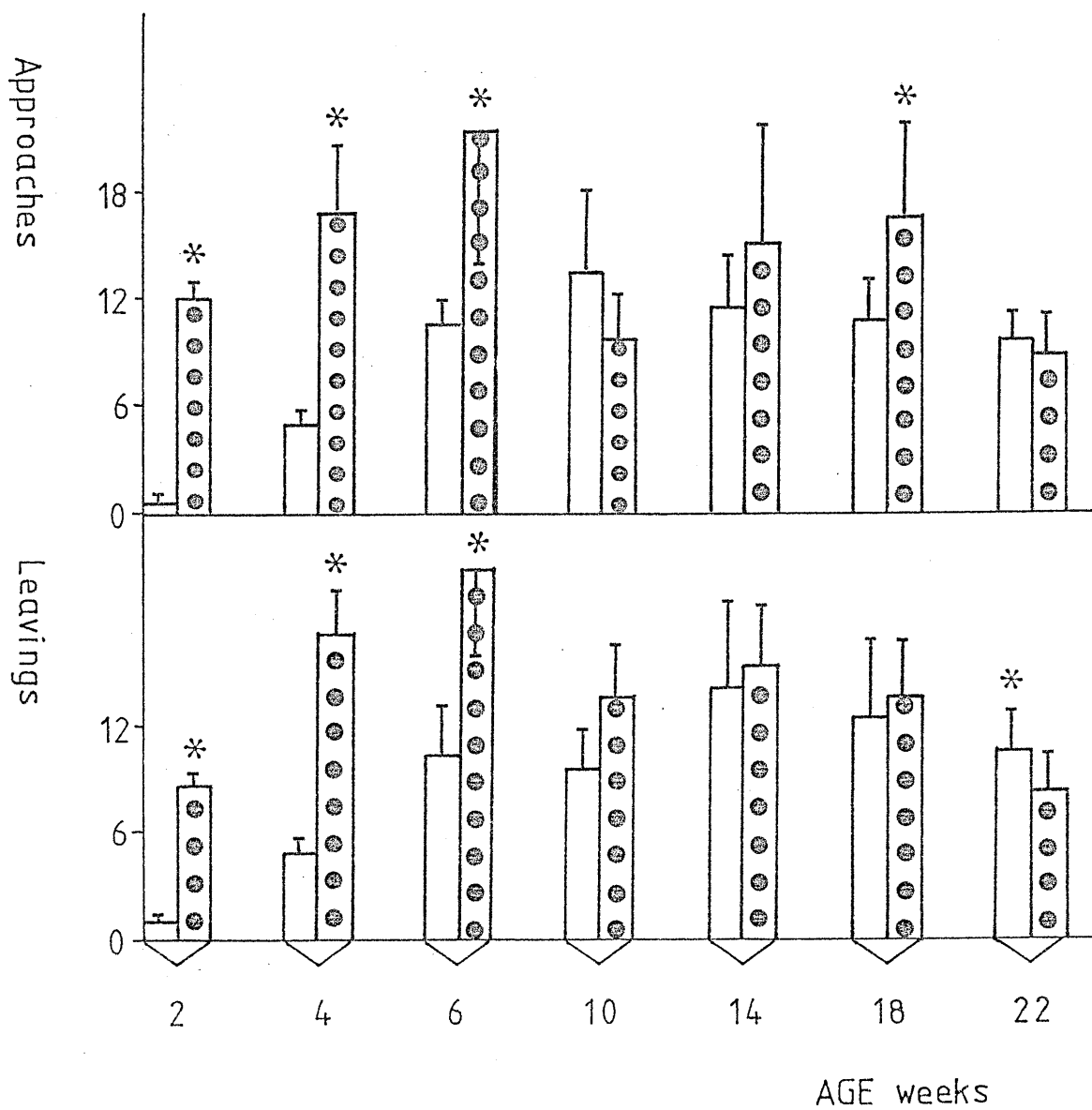
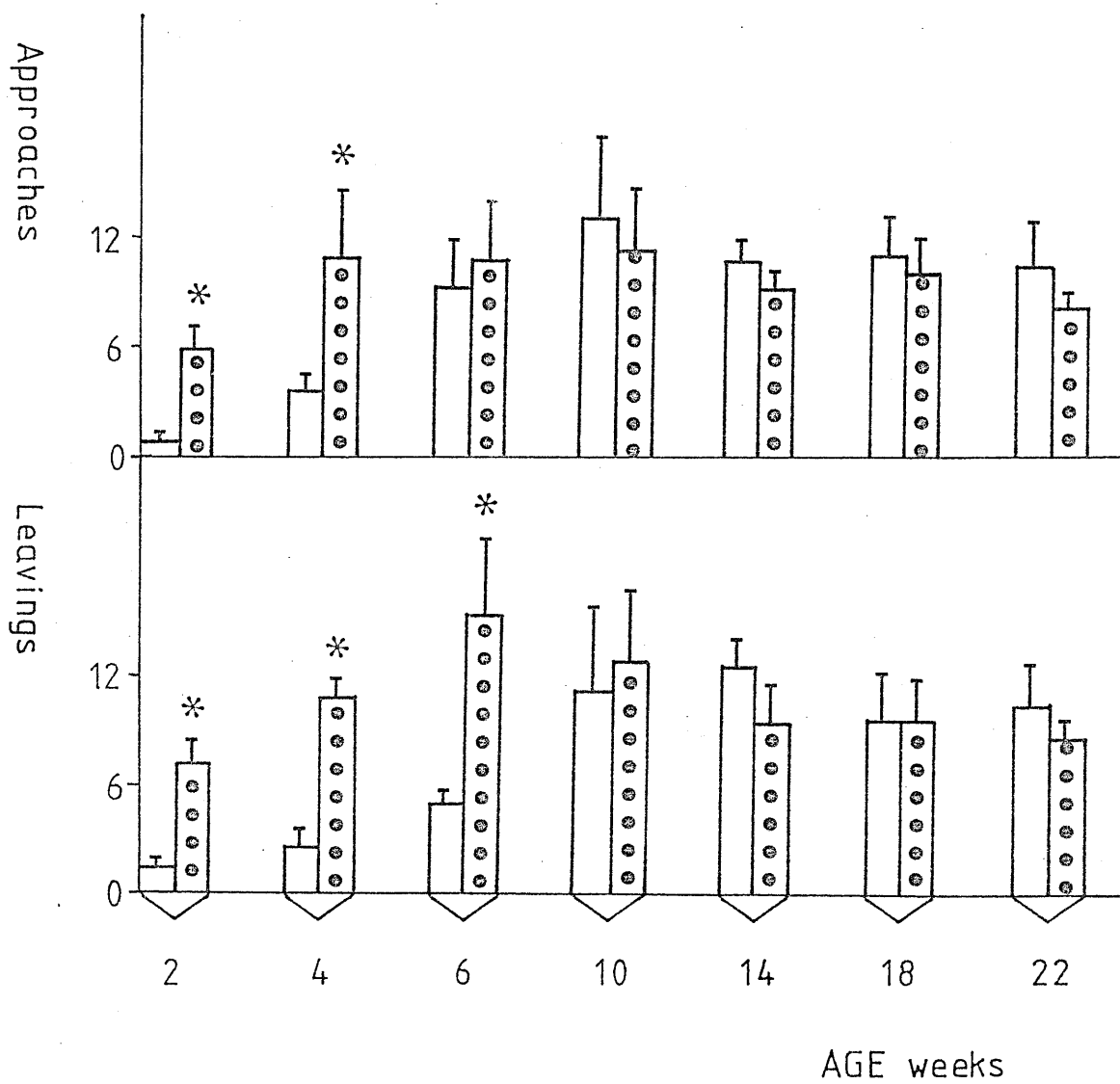


Figure 4.16

Mean frequencies of approaching and leaving between sibling 2's and infants. Conventions as in figure 4.13.



generally not significantly different, each animal playing an approximately equal role in proximity maintenance.

iv) Twins (figure 4.17)

From a low level at 2 weeks, approaching and leaving between infants and twins rises rapidly to a peak at 10 weeks and interactions continue at a high level through to 22 weeks, though frequencies decline slowly from 10 weeks. Responsibility for proximity is shared equally between infants and twins at all ages as would be expected since the twin is also an infant, and the only significant differences between them are at 2 weeks when infants both approach and leave more than twins, and at 6 weeks when infants leave significantly more often than twins.

b) Getting on

As for approaching and leaving above, the mean total %ONS.I - %OFFS.I is shown for all infants in figure 4.18. Twins were never observed to carry infants in Part I so data are combined for fathers, mothers and siblings only. Figure 4.18 shows that overall %ONS.I - %OFFS.I rises steeply to reach 100% at 14 weeks. Infants are not carried after this age. Thus at 2 weeks, while infants are more less immobile, caregivers are responsible for maintenance of time on, but from 4 weeks infants are more important and initiate an increasing proportion of 'ons' and a decreasing proportion of 'offs' until at 14 weeks they are responsible for starting all episodes of time on and for terminating none of them.

i) 'Ons' with each caregiver

Figure 4.19 shows the above data by caregiver, that is, as mean frequencies of initiation and termination of bouts of time on by infants and by caregivers for each caregiver. The figure goes up to 10 weeks only as at 14 weeks only the mother is involved, infants getting

Figure 4.17

Mean frequencies of approaching and leaving between twins and infants.
Conventions as in figure 4.13.

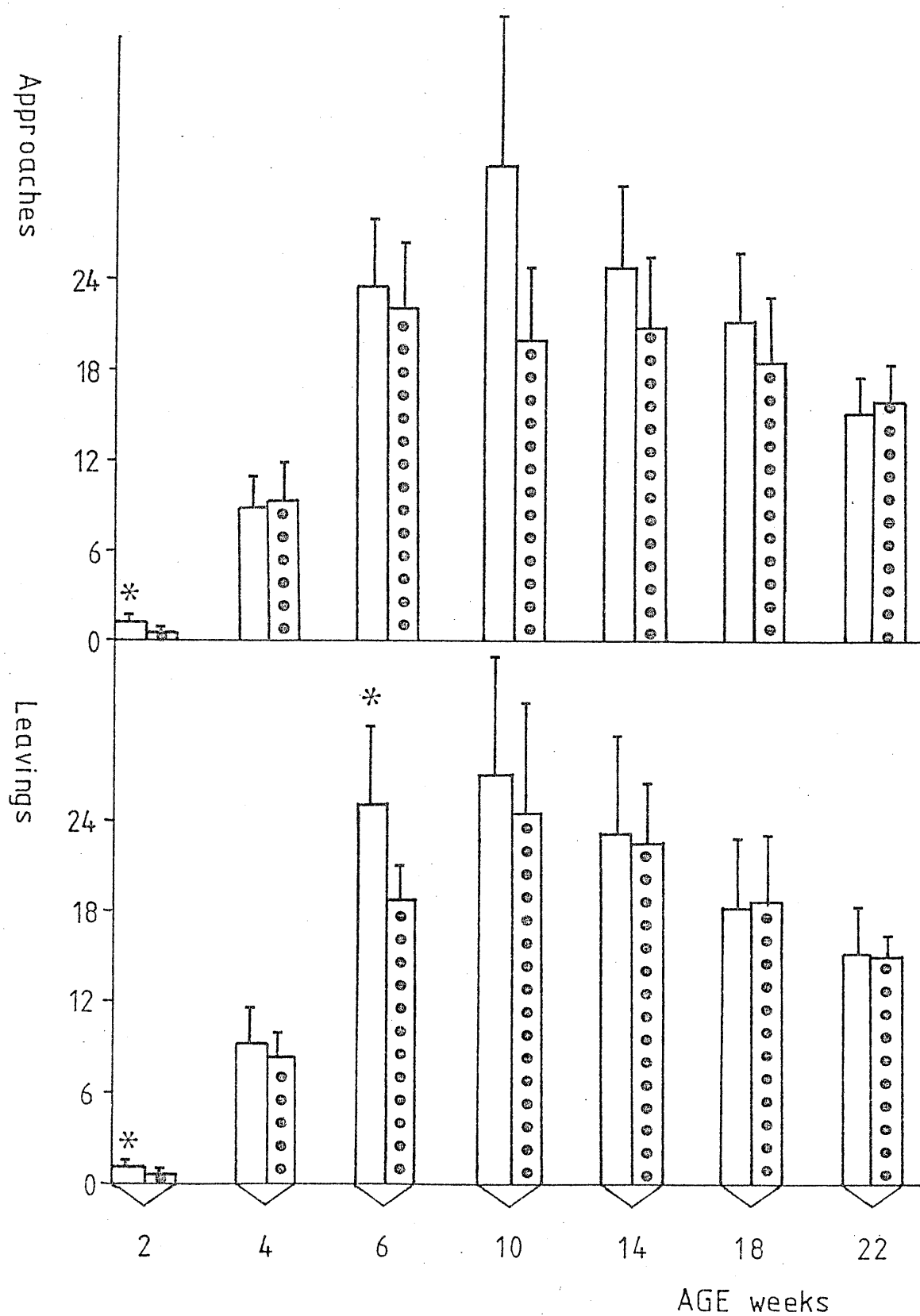


Figure 4.18

Maintenance of time on with all caregivers by infants. Percentage of total initiations of bouts of time on that were made by infants minus percentage of total terminations of bouts of time on by infants, means and standard errors for all infants at each age.

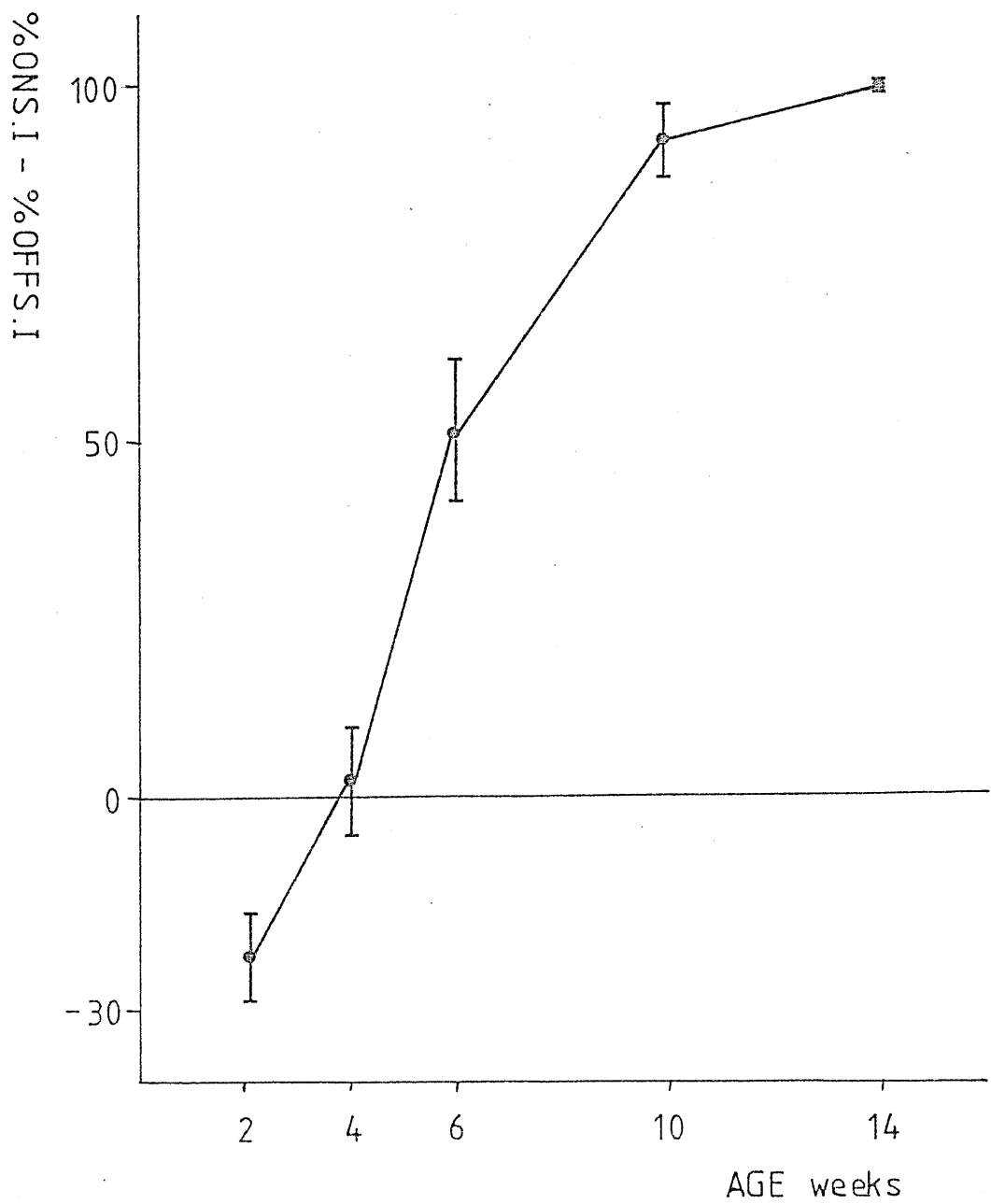
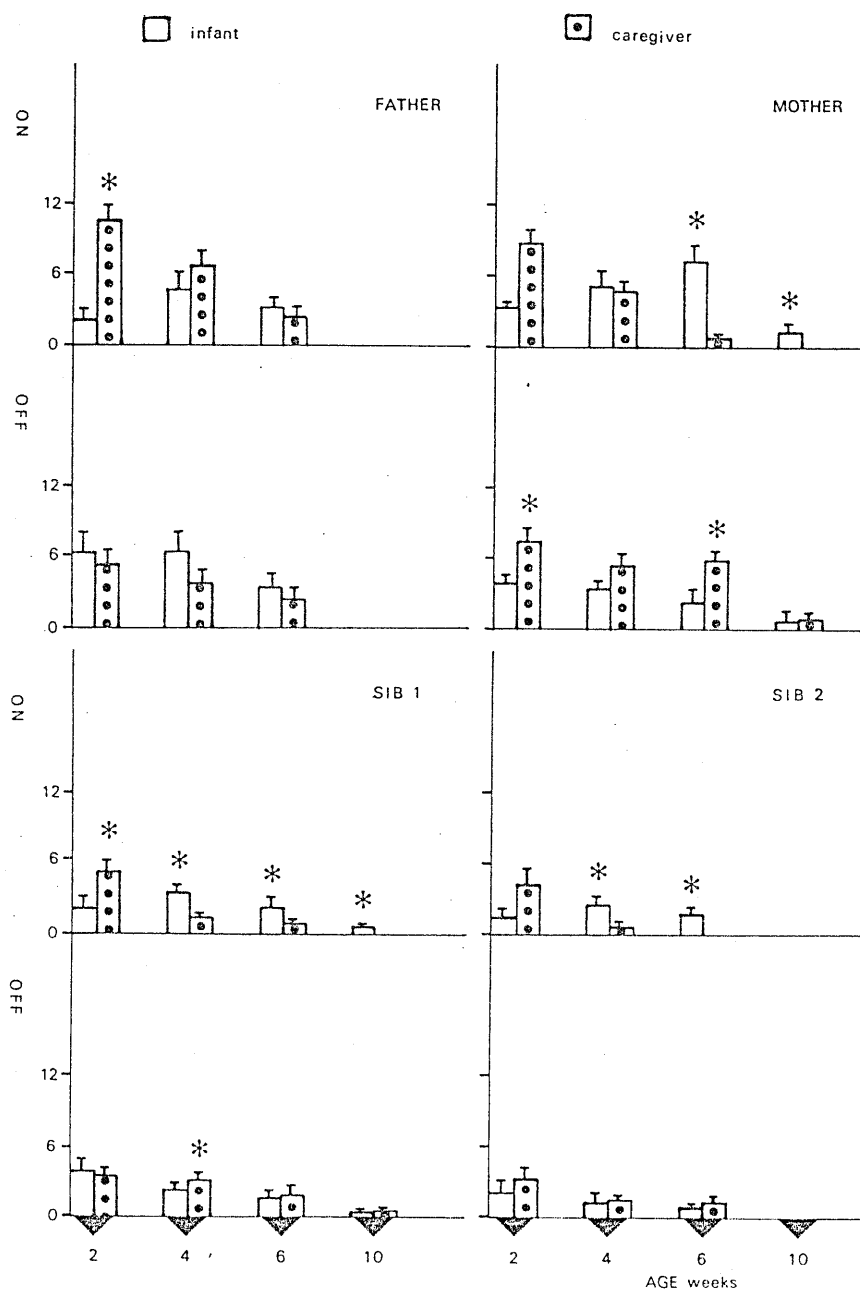


Figure 4.19

Mean number of episodes of time on each caregiver that are initiated and terminated by infants and caregivers. 'On' denotes the initiation of episodes on the caregiver. 'Off' denotes the termination of these episodes. Other conventions as in figure 4.13.



on her a mean of 0.25 times (standard error 0.164) and being rubbed off by her a mean of 0.25 times (standard error 0.164) during the observation period.

The figure shows that all caregivers pick up and carry infants progressively less often and initiate a progressively smaller proportion of carrying episodes from 2 to 10 (14 for mothers) weeks of age. Where differences between frequencies of 'ons' between caregiver and infant are significant (see asterisks on figure 4.19) they show that caregivers pick up infants more often than they get on at 2 weeks, and that infants get on more often than caregivers pick them up from 4 weeks onwards.

'Offs' with each caregiver are dealt with in section c.i).

ii) Infant avoids carry

Figure 4.20 shows the results for the measure 'infant avoids carry'. Changes in absolute frequencies are closely paralleled by changes in relative frequencies, that is, the proportion of all attempts by caregivers to pick up infants which are avoided by infants. For all caregivers there is a very low amount of avoiding at 2 weeks. This rises at 4 weeks, and for fathers rises further at 6 weeks. For other caregivers the measure falls after 4 weeks. The rise at 4 weeks is lowest for mothers and highest for siblings, and overall infants avoid being carried by mothers least and siblings most despite the continued increase in avoidance of fathers. These differences are significant between parents and siblings: The proportion of all attempts by caregivers to pick up infants that are avoided by infants is significantly greater for siblings 1 and 2 than for mothers at 2, 4 and 6 weeks, for sib 1 than father at 4 weeks, and for sib 2 than father at 2 weeks. The differences between fathers and mothers, and between sib 1's and sib 2's are not significant.

Infants do not avoid being carried at all after 6 weeks.

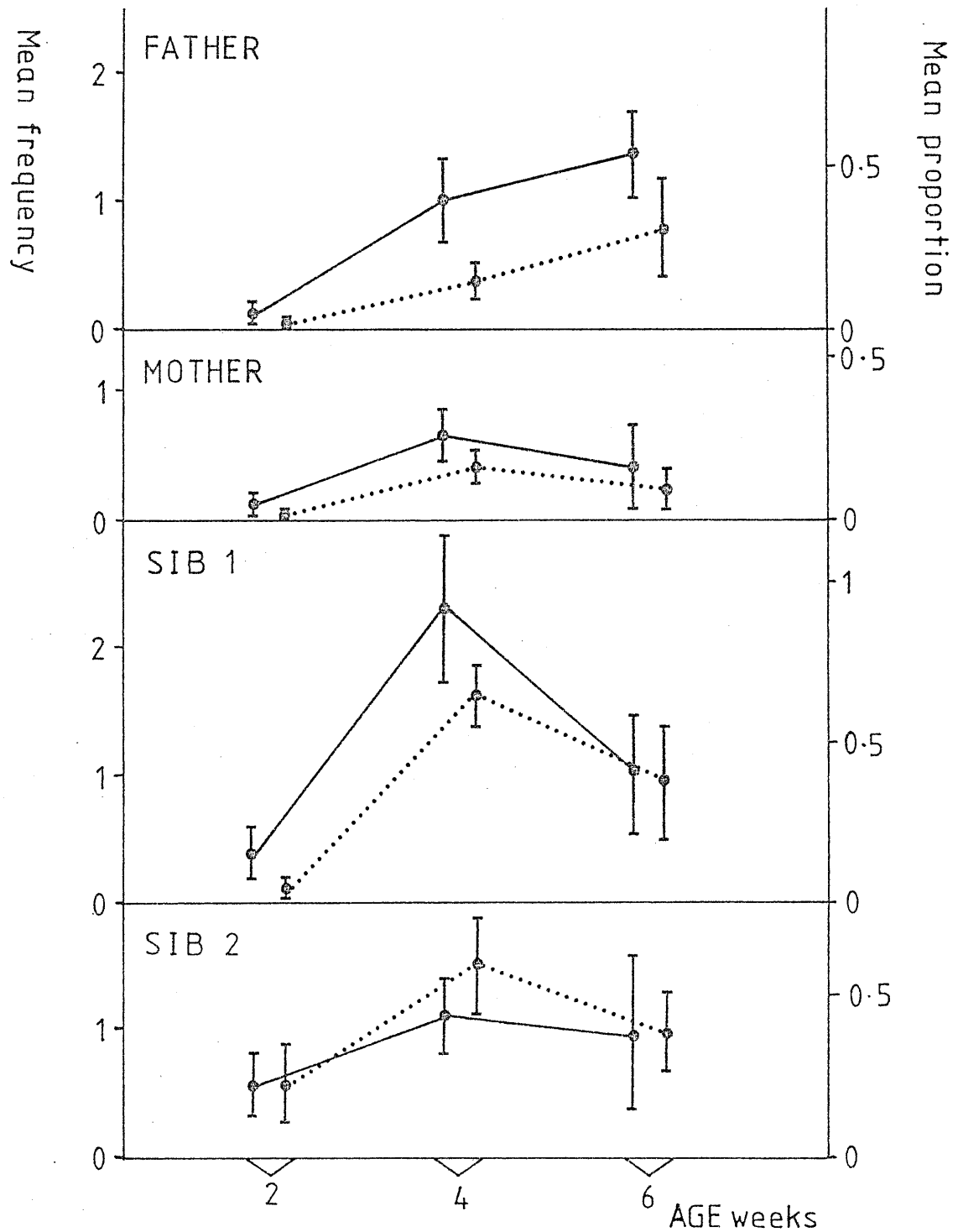
Figure 4.20

Infant avoidance of bouts of time on each caregiver.

Complete line - mean frequency of infants avoiding being picked up by caregivers.

Dotted line - mean proportion of all attempts by caregivers to pick infants up which are avoided by infants.

Vertical bars represent one standard error either side of the mean.



iii) Rejections

Rejections by caregivers of infants' attempts to climb on to them are shown in figure 4.21. The general trend is that the absolute and relative frequency of rejections rises sharply from 2 to 6 weeks and relative rejections continue to rise, though absolute rejections for all caregivers except the mother then fall equally sharply. This is related to the greatly decreased amount of time on at this time (figure 4.2). In more detail, all caregivers except the mother reject all infants' attempts to climb on to them after 10 weeks. Mothers, however, still carry at 14 weeks and thus absolute rejections remain high beyond 6 weeks but relative rejections are not so high as for other caregivers.

The absolute frequency of rejections is significantly higher for mothers than for fathers at 10 weeks, for mothers than sib 1's at 2, 6, 10 and 14 weeks, and for mothers than sib 2's at 2, 4, 10 and 14 weeks. The relative frequency of rejections is significantly lower for mothers than for fathers at 14 weeks, for mothers than sib 1's at 14 weeks, and for mothers than sib 2's at 6, 14 and 18 weeks. All other differences are non-significant.

Table 4.5 shows the difference between different caregivers in absolute frequency of rejections plus 'ons' by infants, i.e. the differences in the total number of attempts by infants to get on to different caregivers at each age. The table shows that infants generally try to get on to mothers significantly more often than any other caregivers.

Figure 4.21

Absolute frequency of rejections (A.F.R., open circles) and relative frequency of rejections (R.F.R., closed circles) of infants by caregivers at different ages. Vertical lines denote standard errors. No R.F.R. is given for sib 1 at 10 weeks or for sib 2 at 14 weeks since at these ages infants made no attempts to climb on to these sibs, so there is no score for the relative frequency of rejections (relative to the number of times infants succeed in getting on).

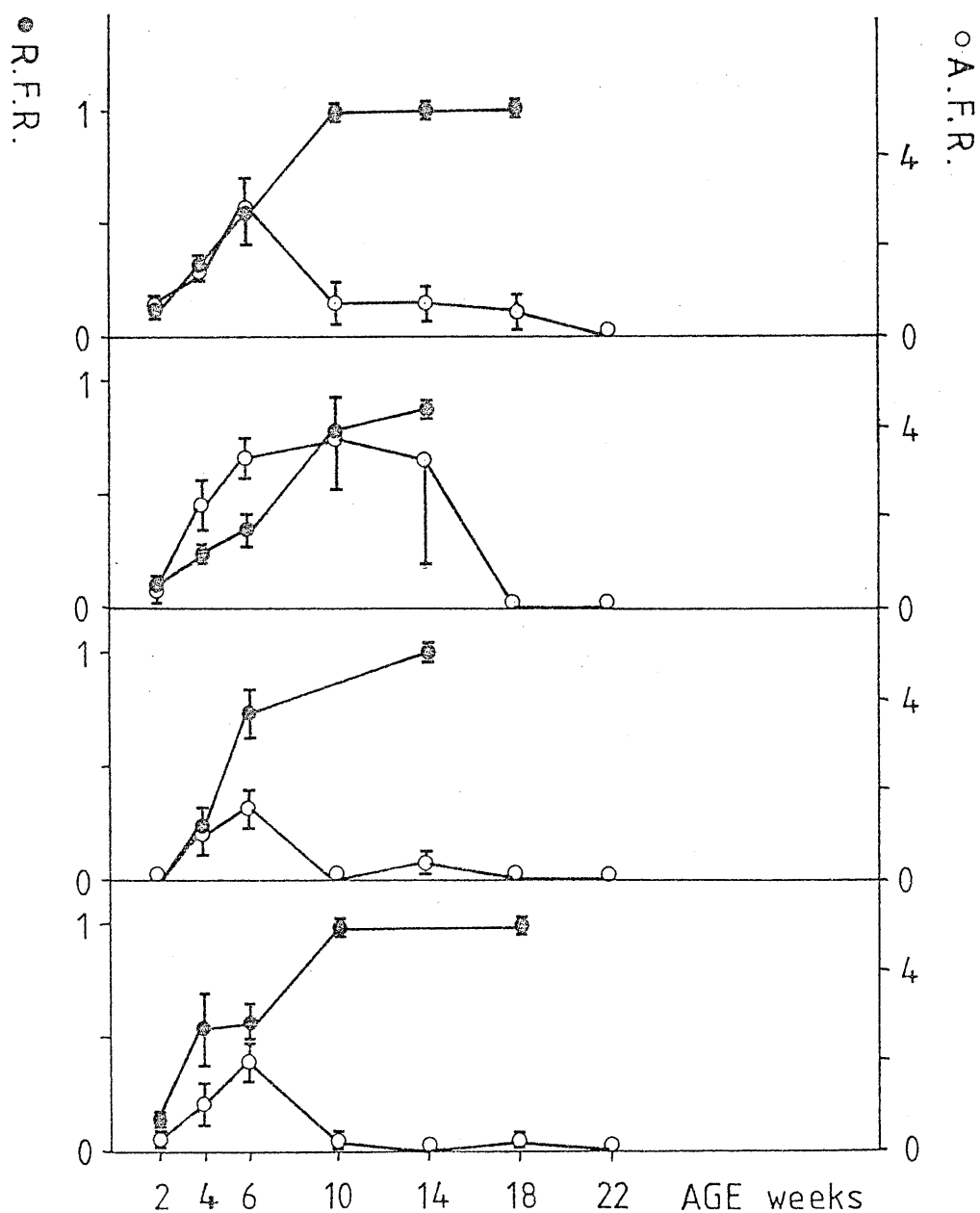


Table 4.5

Differences between caregivers in the number of times infants try to get on to them. Attempts to get on include occasions when the infant tried but failed to get on (rejections), plus occasions when the infant succeeded in getting on. Two-tailed randomization tests with a 5% significance level.

ns not significant. * significant difference in number of attempts to get on to the two caregivers. > more attempts with first caregiver in lefthand column. < more attempts with second caregiver.

CAREGIVERS	AGE/weeks			
	2	4	6	10
Father vs mother	ns	ns	* <	* <
Father vs sib 1	ns	ns	ns	ns
Father vs sib 2	ns	* >	ns	ns
Mother vs sib 1	ns	ns	* >	* >
Mother vs sib 2	* >	ns	* >	* >
Sib 1 vs sib 2	ns	ns	ns	ns

c) Getting off

i) 'Offs' with each caregiver

Figure 4.19 also shows the mean frequency of termination of bouts of time on ('offs') by caregivers and by infants. Both infants and caregivers show a decrease in frequency of 'offs' from 2 to 10 weeks, but the proportion of bouts terminated by each varies. In the case of time on fathers, infants tend to terminate a higher proportion of bouts than fathers but the difference is not significant at any age. Time on mothers is more often terminated by mothers than infants, and this is significant at 2, 6 and 14 weeks of age. Proportions of bouts of time on terminated by siblings and by infants fluctuate from age to age but there are no significant differences between infants and siblings except at 4 weeks when sib 1's perform a significantly higher proportion of 'offs' than infants.

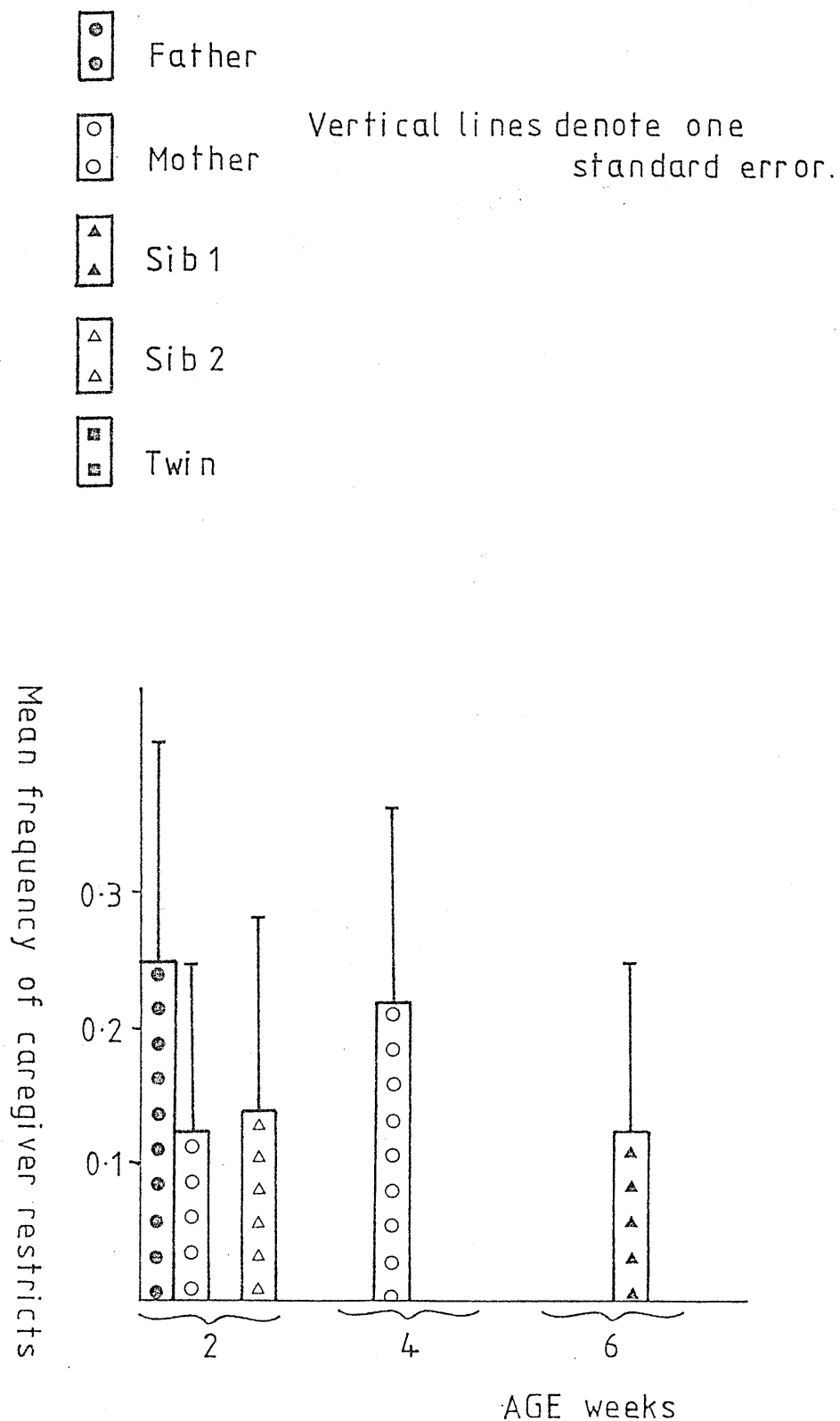
Combining data for 'offs' with data for initiations of bouts of time on (section b.i) above), it can be seen that though all caregivers are responsible for time on at 2 weeks, after this only fathers remain important in maintenance of time on. By 6 weeks fathers and infants play about equal roles, but for all other caregivers the infant is now more important. Thus, while fathers are still "interested" in carrying infants up to 6 weeks, for all other caregivers it is up to the infant to get on them.

ii) Caregiver restricts

The behaviour 'caregiver restricts' an infant's attempt to get off occurred on very few occasions, far fewer than reported for rhesus monkeys (Hansen, 1966; Harlow et al, 1963; Hinde & Spencer-Booth, 1967 a & b) or pigtail and bonnet macaques (Rosenblum, 1971). Figure 4.22 shows the mean frequency of restrictions performed by caregivers. The

Figure 4.22

Mean frequency of attempts by caregivers to prevent infants from getting off of them.



behaviour was not seen to occur after 6 weeks of age and was performed in only two of the three families and towards only three out of the nine infant subjects. This accounts for the large standard errors in figure 4.22. The fathers involved restrict at 2 weeks only, the mothers at 2 and 4 weeks, while one sib 1 restricts at 6 weeks, and its twin, the sib 2, restricts at 2 weeks. In view of the very small amount of data on this behaviour, the only conclusions which can be drawn are that restriction of infants' attempts to get off is very rare and occurs only in the early weeks of life (2 to 6) during the period when the infant is spending a lot of its time on caregivers.

For those infants which were restricted table 4.6 shows what proportion of their attempts to get off were restricted. From 2 to 6 weeks, where restrictions occur they form an increasing proportion of infants' attempts to get off. However the data are far too sparse for generalisations and are as likely to be a function of caregiver as of age of the infant. Restraining young infants' attempts to leave their caregivers is probably a protective behaviour and in macaques would prevent infants being harmed by other animals in the troop. In a marmoset group all individuals are closely related (a family) and all help look after the young. Protective behaviour of this type is therefore much less important and would not be expected to occur very often.

iii) Caregiver fails to rub off

Figure 4.23 shows the mean frequency of occurrence of caregivers attempting but failing to rub infants off. Failures to rub off occur with decreasing frequency from 2 to 10 weeks after which none occur (infants are no longer carried by any caregiver except the mother after 10 weeks and she does not fail to rub off at this age). Frequencies tend to be lower for siblings than parents. The decrease

Table 4.6

Proportion of each infant's attempts to get off that were restricted.
Only infants that were restricted included.

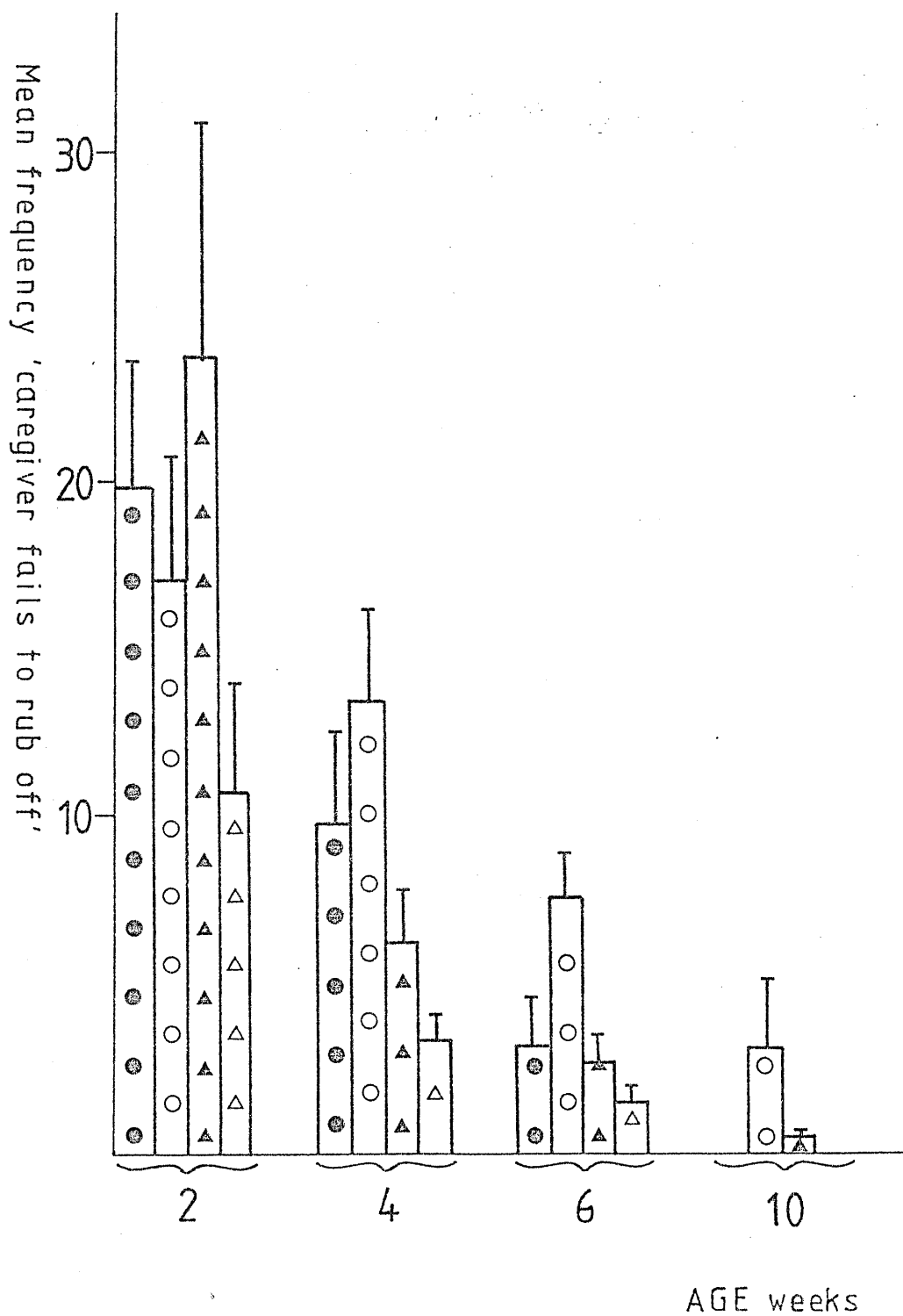
Figures in brackets are total frequencies of infants' attempts to get off.

SUBJECT	CAREGIVER RESTRICTING	AGE/weeks		
		2	4	6
1	Father	0.125 (8)	0 (7)	0 (3)
	Mother	0 (4)	0.200 (5)	0 (5)
	Sib 1	0 (7)	0 (2)	0.333 (2)
	Sib 2	0.167 (6)	0 (3)	0 (2)
4	Mother	0 (4)	0.143 (6)	-
6	Father	0.083 (12)	0 (10)	0 (7)
	Mother	0 (4)	0.167 (6)	-

Figure 4.23

Mean frequency of failed attempts by caregivers to rub infants off.

Conventions as in figure 4.22.



for fathers is faster than that for mothers. Fathers fail to rub off significantly more than sib 2's at 4 weeks, mothers significantly more than fathers at 6 and 10 weeks, more than sib 1's at 6 weeks and more than sib 2's at 6 and 10 weeks. All other differences between caregivers are non-significant.

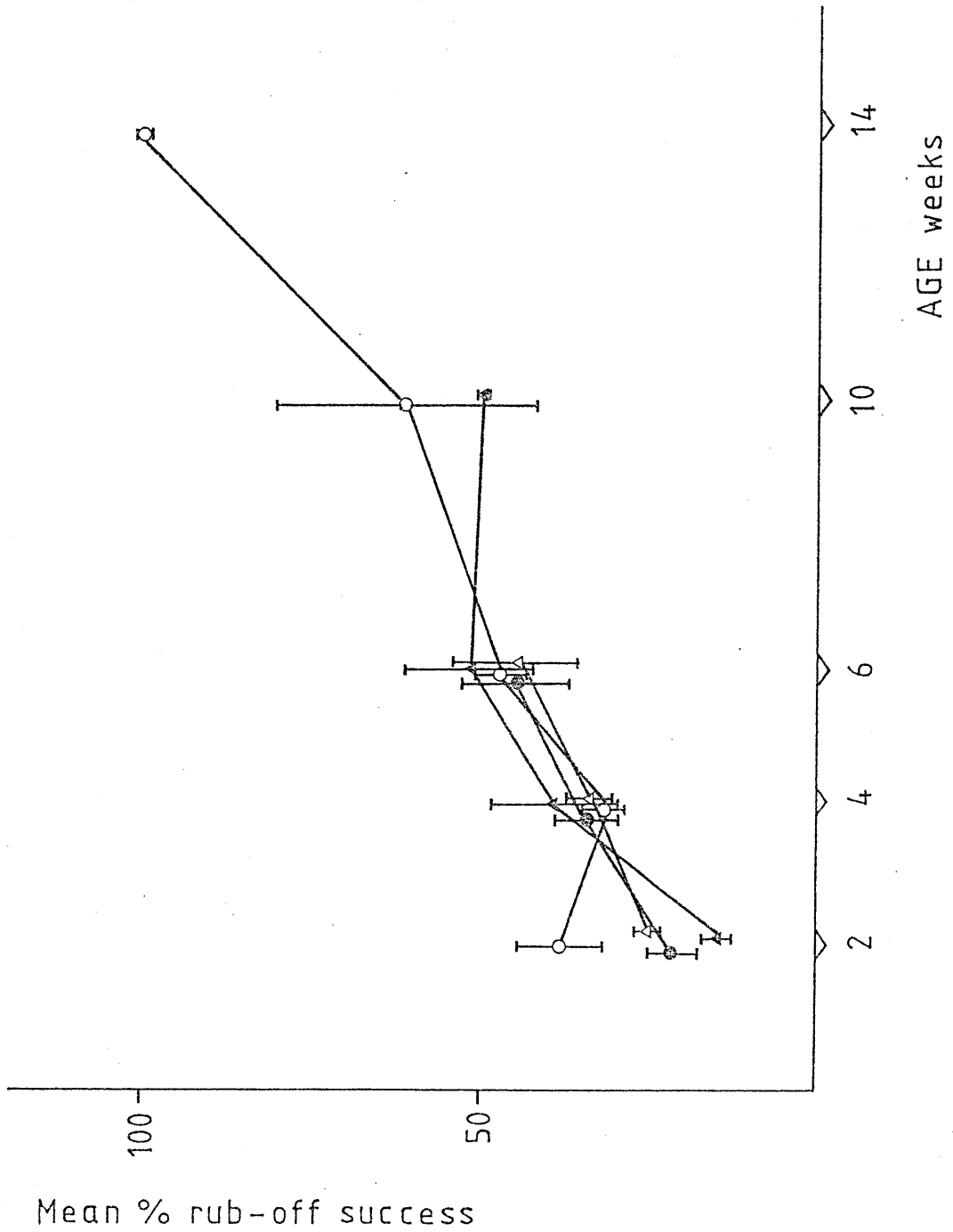
The decrease in fails to rub off may be partly accounted for by the decrease in time on over this period (see figure 4.2) hence there is less opportunity for attempting to rub infants off.

In addition, the decrease may be due to caregivers getting better at rubbing infants off as infants get older. Figure 4.24 shows the mean percentage rub-off success of caregivers, that is, the number of successful rub-offs as a percentage of rub-offs plus failures to rub off. As can be seen from the diagram, rub-off success increases steadily with age, with all caregivers showing very similar success rates. At 2 weeks mothers are most successful (significantly so) and reach 100% success at 14 weeks, by which time very little time is spent on but all attempts by mothers to remove infants are successful. The large standard error apparent for mothers at 10 weeks is a consequence of there being only four data points here (only four out of nine infants spent any time on their mothers at 10 weeks), so the point is the mean from four infants.

The increase in rub-off success could be due to the caregivers improving or to the infants becoming easier to dislodge (or both). Infants could be easier to dislodge because they are larger and present a bigger area to push against, because they become less skilled at holding on, or because they are less motivated to hang on. This will be discussed further in section 4.5).

Figure 4.24

Mean percentage of all attempts by caregivers to rub infants off which are successful. Conventions as in figure 4.1.



4.4) RESULTS 3 - Other events

a) Tantrums

The total number of tantrums shown by infants declines with age, as is shown in table 4.7. Figure 4.25 shows the mean percentage of all tantrums by infants occurring with different caregivers at each age. There is a general decrease with age for all caregivers, the particularly low value for twins at 2 weeks being due to the rarity of

Table 4.7

Mean total frequency of tantrums shown by infants at each age.

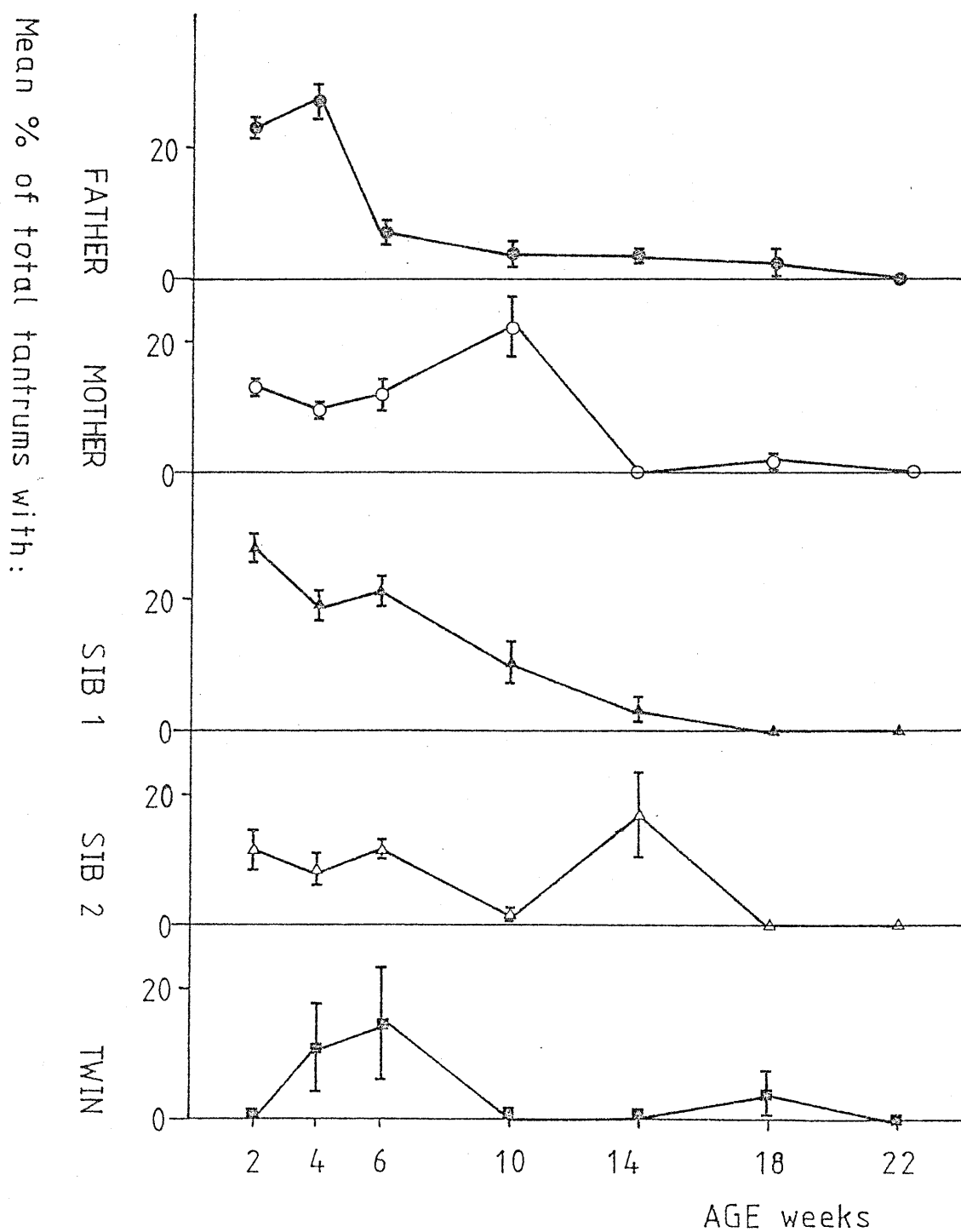
	AGE/weeks						
	2	4	6	10	14	18	22
MEAN	101.00	40.33	39.75	16.25	3.50	2.00	0.00
STANDARD ERROR	27.59	6.65	15.31	6.78	2.15	1.48	0.00

interactions between infants and their twins at this age, as noted in section 4.2a) above. (The apparent peaks for mothers at 10 weeks, sib 2's at 14 weeks and twins at 18 weeks are each due to one particularly large data point in each case.)

Though more tantrums appear to occur with fathers and with sib 1's in the early weeks, no one caregiver seems to be particularly associated with tantrums at any age. Differences in percentage of tantrums with fathers, mothers and siblings are generally non-significant, the only significant differences being fathers more than mothers at 10 weeks and less than sib 2's at 14 weeks, mothers less than sib 2's at 14 weeks,

Figure 4.25

Mean percentage of total tantrums by infants that occurred with each caregiver. Conventions as in figure 4.1.



sib 1's more than sib 2's at 10 weeks and less than sib 2's at 14 weeks. Twins, however, are associated with significantly fewer tantrums than all other caregivers at 2 weeks, and significantly fewer than mothers and sib 1's at 10 weeks.

b) Ignores

Figure 4.26 shows the mean frequency of ignores by each caregiver of infants at each age. Fathers and mothers ignore more than siblings (significantly so from 10 weeks for fathers and from 2 weeks for mothers), and more than twins (significant at all ages except 4 weeks). Twins ignore infants significantly less than parents and siblings except at 2 weeks, and ignore only at 4, 6 and 10 weeks. Table 4.8 shows in detail which differences are significant. Ignores by fathers peak at 10 weeks, as do those by siblings, while mothers' ignores peak at 6 weeks.

c) Food-stealing

Figure 4.27 shows the mean frequency of attempts (successful and unsuccessful) at food-stealing from caregivers by infants. In general it can be seen that attempts to steal food increase with age to a peak at around 10 weeks, and then decline. No food-stealing occurs at 2 weeks of age. Food-stealing from fathers remains low (less than 0.5 attempts) at all ages. Attempts from mothers rise sharply to a plateau at 10 and 14 weeks and then drop off to about the 4 week level by 22 weeks. Attempts from both siblings peak at 10 weeks and again drop off to a low level by 22 weeks. Food-stealing from twins does not occur until 6 weeks of age, possibly as before this the twin (also an infant) does not have any food itself to be stolen, and occurs only at a low level.

Figure 4.26

Mean frequency with which different caregivers ignored infants.

Each vertical line denotes one standard error

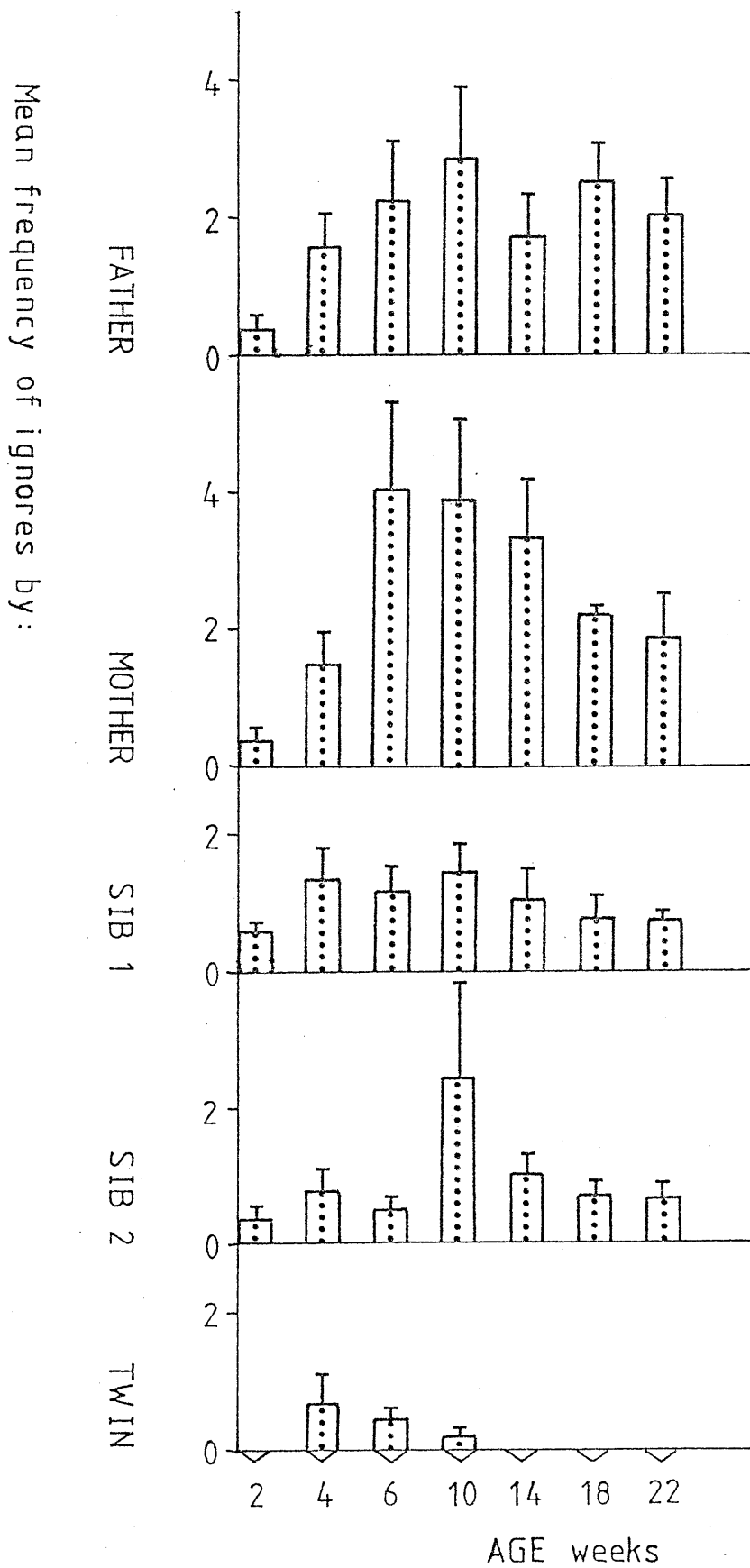


Table 4.8

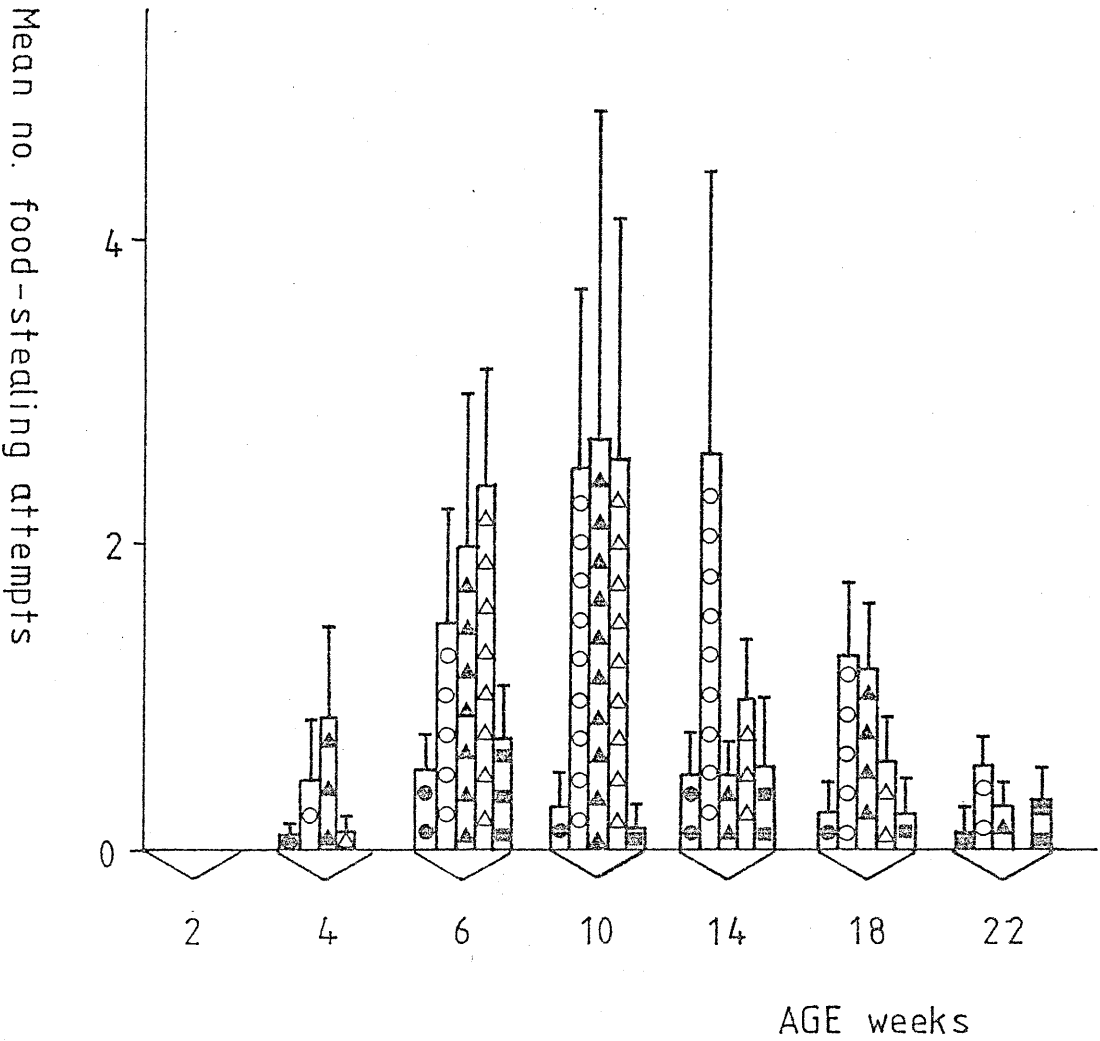
Differences between caregivers in the number of times they ignore infants at each age. Two-tailed randomization tests with a 5% significance level.

ns not significant. * significant difference in number of ignores between the two caregivers. > more ignores with first caregiver in lefthand column. < more ignores with second caregiver.

CAREGIVERS	AGE/weeks						
	2	4	6	10	14	18	22
Father vs mother	ns	ns	ns	ns	* <	ns	ns
Father vs sib 1	ns	ns	ns	* >	ns	* >	* >
Father vs sib 2	ns	ns	ns	ns	ns	* >	ns
Father vs twin	* >	ns	* >	* >	* >	* >	* >
Mother vs sib 1	* <	ns	* >	* >	* >	* >	ns
Mother vs sib 2	* >	* >	* >	ns	* >	* >	ns
Mother vs twin	* >	ns	* >	* >	* >	* >	* >
Twin vs sib 1	* <	ns	* <	* <	* <	* <	* <
Twin vs sib 2	* <	ns	ns	* <	* <	* <	* <
Sib 1 vs sib 2	ns	ns	ns	ns	ns	ns	ns

Figure 4.27

Mean frequency of attempts (successful and unsuccessful) by infants to steal food from caregivers. Conventions as in figure 4.22.



The frequency of food-stealing attempts from twins is significantly less than attempts from fathers at 4 weeks, from mothers at 4 and 10 weeks, from sib 1's at 4, 6 and 10 weeks, and from sib 2's at 4, 6, 10, 14, 18 and 22 weeks. Food-stealing attempts from fathers occur significantly less often than attempts from mothers at 10 and 18 weeks, from sib 1's at 6 and 18 weeks, and from sib 2's at 6 weeks. Attempts are made from fathers significantly more than from mothers at 22 weeks, and from mothers significantly more than sib 2's at 22 weeks. Other differences are not significant.

Figure 4.28 shows, for frequencies of food-stealing summed over all infants at each age (as frequencies are very low), the percentage success at food-stealing from each caregiver (the total frequencies are also given in figure 4.28). Similar trends are seen for all caregivers. Success drops to a low from 6 or 10 weeks than rises again from about 14 weeks. It seems likely that food-stealing success rises at later ages as infants are much bigger and more able to withstand caregivers' attempts to prevent them stealing food. At earlier ages (2 to 6 weeks) caregivers do not appear actively to prevent food-stealing attempts, and failures are due to the ineptitude of the infants. The drop in success at 10 weeks will be discussed in section 4.5).

d) Aggression

Figure 4.29 shows the mean frequency of aggressive acts by caregivers towards infants. Aggressive acts include rub-offs and rejections which involve hard biting and lunging, threats ("erh-erh" vocalizations and ruffling of the fur, see Stevenson and Poole, 1976) usually while holding food, and lunging with grasping and biting.

Aggression by all caregivers is rare and twins do not show it at all. Mothers show the highest peak of aggression, this is at 10 weeks and is significantly higher than aggression by other caregivers. Sibling

Figure 4.28

Percentage success of total food-stealing attempts by all infants from each caregiver at each age. Data from all infants summed at each age. Figures below graph are summed frequencies of food-stealing by all infants from each caregiver at each age.

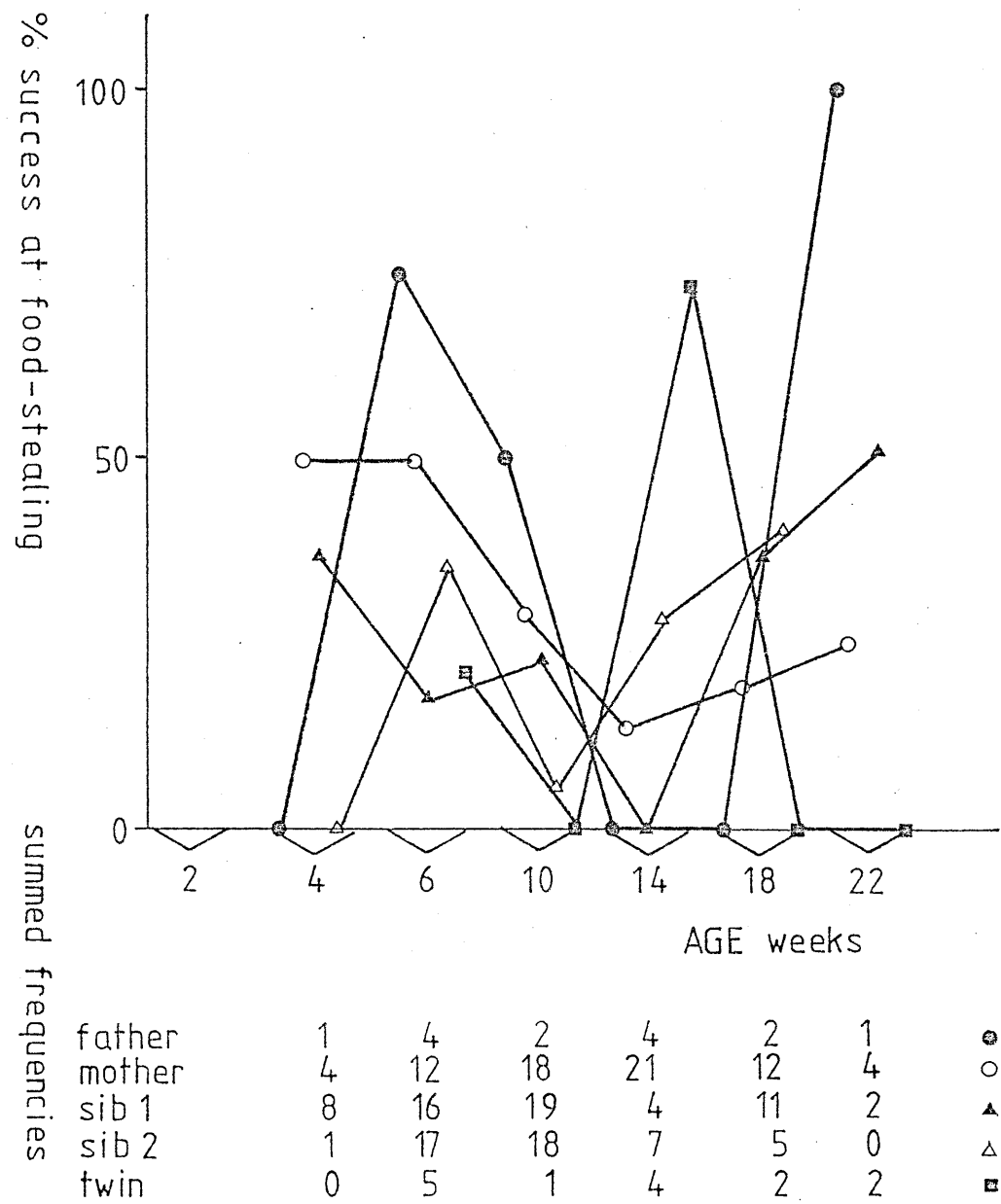
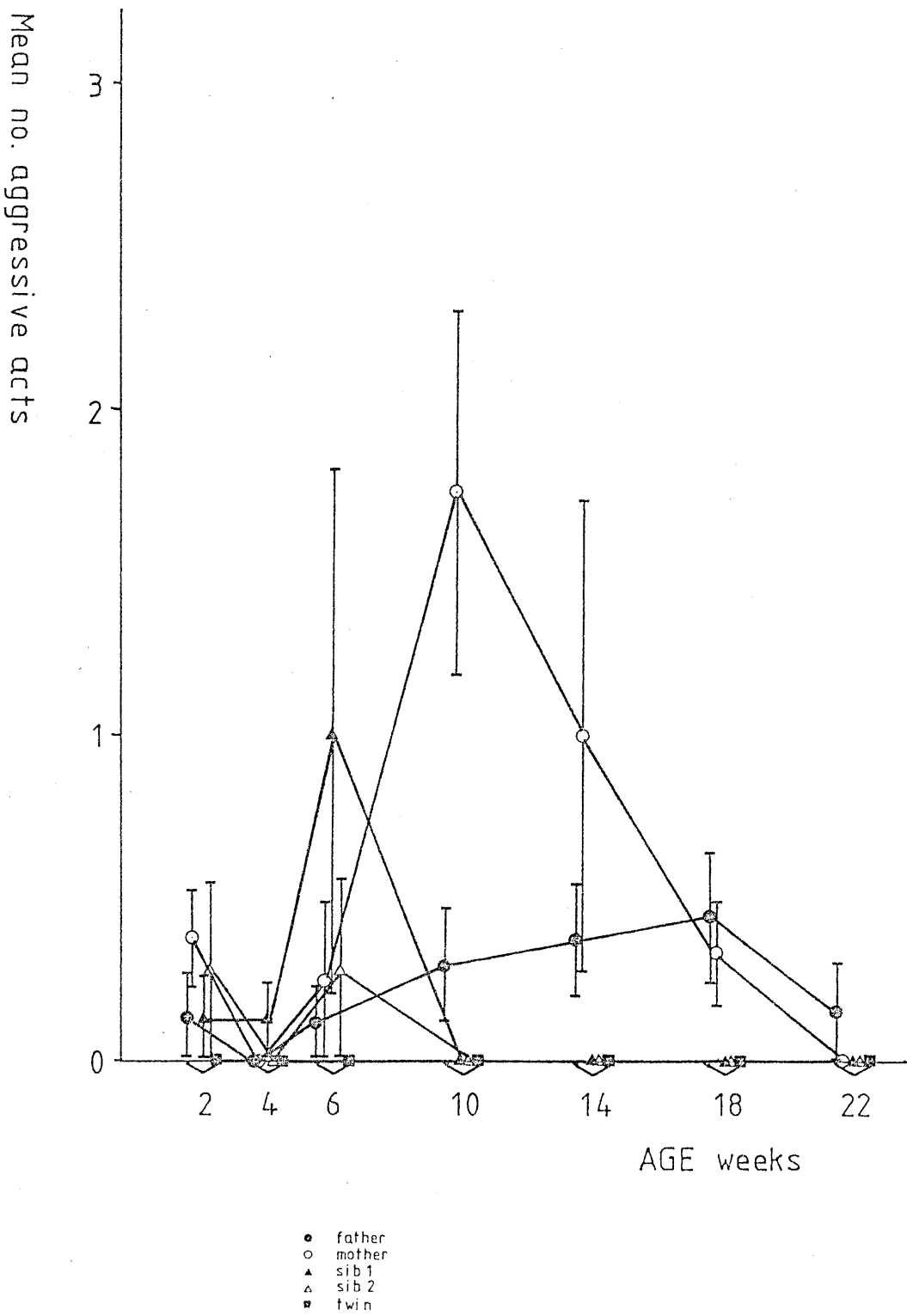


Figure 4.29

Mean frequency of aggressive acts by caregivers towards infants at each age. Conventions as in figure 4.1.



aggression peaks at 6 weeks and that by sib 1's is significantly higher than aggression by fathers and twins, though not significantly different from that by mothers or sib 2's. After 6 weeks, only parents show aggression against infants, mothers significantly more than fathers at 10 weeks and fathers significantly more than mothers at 22 weeks.

In summary, all caregivers except twins show aggression against infants from 2 to 6 weeks, and after this age only parents are aggressive.

e) Data taken at 22 weeks only

The data described here were taken to form part of a composite 'social competence score' to be discussed in section 4.8). Here the data will just be presented.

Figure 4.30 shows the mean frequency with which infants attempted to pick up and rub off, successfully and unsuccessfully, the younger siblings born into their families. In this case, data are means of four infants only because in four cases new infants had not been born by 22 weeks, and in one case the subject infant made no attempts at all to handle the new babies. The figure shows that on average the infants were 61% successful at picking up babies but only 20% successful at rubbing them off.

Figure 4.31 shows the mean frequency of interruptions by infants of caregivers, and by caregivers of infants. Caregivers are significantly more successful at interrupting infants (65.9%) than infants are at interrupting caregivers (40.7%).

Figure 4.30

Mean frequency of subject infants' attempts to pick up and rub off their own infant siblings. Dotted columns represent successful attempts, empty columns represent unsuccessful attempts. Vertical bars denote standard errors.

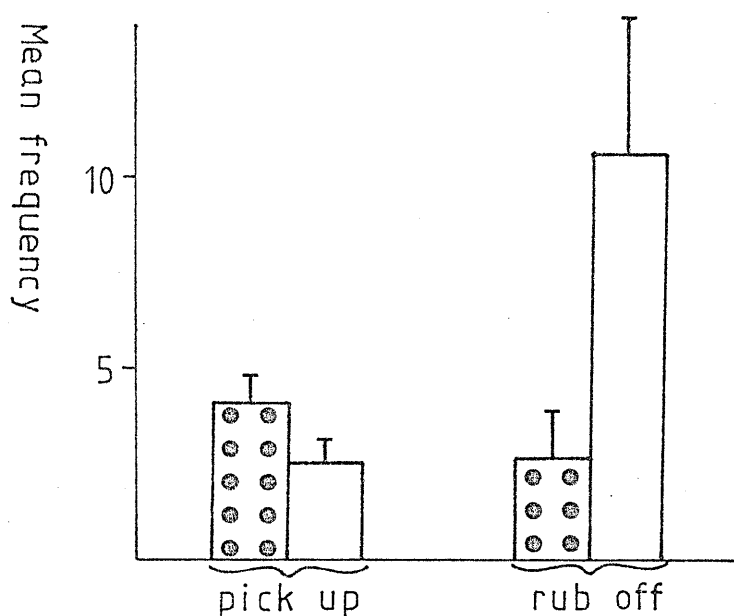
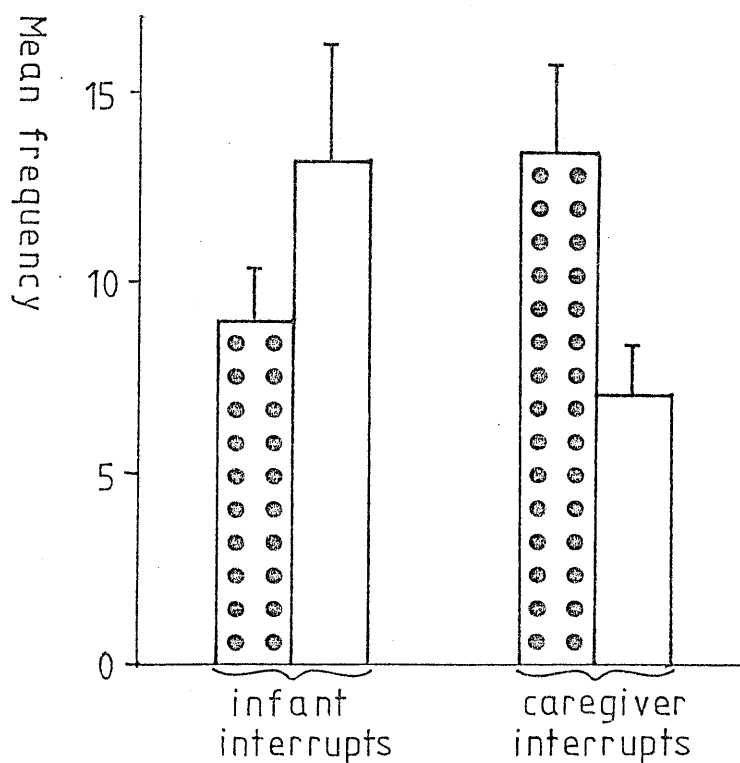


Figure 4.31

Mean frequency of attempts by infants to interrupt caregivers, and by caregivers to interrupt infants ongoing behaviour. Conventions as in figure 4.30.



4.5) INTERPRETATION OF RESULTS

From the data presented above, a brief summary of the form of infant social development from 2 to 22 weeks is as follows: Time with all family members decreases sharply from 2 to 6 weeks but the decline is less dramatic for mothers and for twins. This is because while time on declines to zero, time in contact with mothers and twins increases. Time playing with twins also increases at this time. As contact with mothers and twins later decreases, play with siblings increases. These features will be investigated in section a) below where data on different behaviours are compared, with a view to explaining the changes in terms of a small number of behavioural tendencies on the part of the caregivers and infants. Section b) deals with the effects of handling on the behaviour of sibling 1 as opposed to sibling 2. The change in responsiveness of caregivers to infants as they get older is dealt with in section c), and section d) concentrates on the meshing of caregivers' and infants' behaviour, and on compensation between caregivers.

a) Responsibility for changes in behaviour with age

This section analyses how behaviours are distributed amongst different caregivers by comparing the relative changes in occurrence of different behaviours with each caregiver. It thereby tries to explain whether such changes are due to changes in the behaviour of caregivers or of infants. It is arranged in sections dealing with the changes in time on, in contact, and playing.

i) The decrease in time on caregivers from 2 to 10 weeks

Most of the time spent with caregivers during the first 6 weeks of life is spent on them. When infants are too old to be carried by their mothers they tend to spend time in contact with them, whereas they do not

stay in contact with other caregivers who have stopped carrying them. Infants continue to spend time in contact with their twins after parents and siblings have ceased carrying them. This can be seen by comparing figures 4.1, 4.2 and 4.6. Figure 4.11 shows that as infants cease to be carried more time is spent in contact. Figure 4.6 shows that while the amount of time spent in contact with fathers and siblings remains low (less than 0.5%) throughout the 22 weeks, the percentage of time spent in contact with twins rises to a peak of 6.2% at 4 weeks and that with mothers rises to a peak of 3% at 14 weeks.

Infants with rejecting parents tend to spend more time with their twins than infants with less rejecting parents, but rejections by siblings do not have this effect. Correlations between absolute and relative frequencies of rejection and time spent with twins (table 4.9) show that infants with highly rejecting fathers spend more time with their twins than do infants with less rejecting fathers. They do not however spend more time on their mothers or siblings than infants with less rejecting fathers (table 4.10). Similarly, 4 week old infants with rejecting mothers spend more time with twins than do 4 week old infants with less rejecting mothers, but they do not spend more time on fathers and siblings. No significant correlations were found between rejection rates by siblings and time spent on other caregivers or with twins. Negative correlations between absolute and relative frequencies of rejection by caregivers and time infants spend on the same caregivers show that infants tend to spend least time on caregivers who are most rejecting (table 4.10).

The decrease in the amount of time infants spend on caregivers appears to be due mainly to changes in the behaviour of the caregivers. Caregivers become less responsible for time spent on with increasing age of the infants (figure 4.18). They pick up and carry infants

Table 4.9

Spearman rank order correlation coefficients between rejection frequencies by caregivers and time with twin. Upper of each pair of figures refers to 4 week old infants, lower to 6 week old infants.

* $p < 0.05$. ** $p < 0.01$.

ABSOLUTE FREQUENCY OF REJECTIONS BY:	TIME WITH TWIN
Father	0.95 ** 0.90 **
Mother	0.71 * 0.35
Siblings	0.26 -0.13
RELATIVE FREQUENCY OF REJECTIONS BY:	TIME WITH TWIN
Father	0.84 ** 0.75 *
Mother	0.71 * 0.13
Siblings	0.42 -0.43

Table 4.10

Spearman rank order correlation coefficients between frequencies of rejections and rub-offs by caregivers and time on caregivers.

Conventions as in table 4.9.

ABSOLUTE FREQUENCY OF REJECTIONS BY:	TIME ON:		
	Father	Mother	Siblings
Father	-0.81 **	0.49	-0.40
	-0.32	-0.17	0.54
Mother	-0.71 *	0.25	-0.37
	-0.57	-0.87 **	-0.16
Siblings	-0.34	0.03	-0.31
	0.17	0.23	0.45
RELATIVE FREQUENCY OF REJECTIONS BY:			
	Father	Mother	Siblings
Father	-0.87 **	0.39	-0.75 *
	-0.93 **	-0.76 *	-0.14
Mother	-0.77 *	0.39	-0.22
	-0.58	-0.71 *	-0.08
Siblings	-0.48	-0.15	-0.45 *
	-0.12	-0.35	-0.60 *
NUMBER OF RUB-OFFS BY:			
	Father	Mother	Siblings
Father	0.63 *	-0.51	0.55
	0.60	0.84 **	0.35
Mother	-0.23	0.00	-0.40
	0.55	0.84 **	0.72 *
Siblings	0.59	-0.32	0.39
	0.14	0.61	0.56 *

progressively less often and initiate a progressively smaller proportion of carrying episodes from 2 to 6 weeks (figure 4.19). Results of Spearman correlations between mean time on caregivers and mean frequency of pick-ups by caregivers and getting on by infants are given in table 4.11. Time on is not in general related to the number of times infants get on to caregivers, but is positively related to the number of times mothers and siblings pick up infants at 2 weeks, and the number of times fathers pick up infants at 4 and 6 weeks, and inversely related to the number of times sibling 2's pick infants up at 6 weeks. This is in line with figure 4.19 which suggests that infants take over responsibility for time on mothers and siblings, but come to share responsibility with fathers.

There is a decrease in the number of times infants avoid being carried by all caregivers except fathers between 4 and 6 weeks (figure 4.20). This also suggests that a certain amount of the decrease in time on fathers may be due to infants (as infants increase their avoidance of being picked up by fathers between 4 and 6 weeks), however frequency of infant avoids carry by fathers and time on fathers are not significantly correlated at 6 weeks ($r_s = 0.411$, $p > 0.05$).

Mothers and siblings are most aggressive towards infants around 6 and 10 weeks (figure 4.29), fathers and siblings ignore infants most at 10 weeks and mothers ignore most at 6 weeks (figure 4.26).

The number of times caregivers successfully rub off infants does not increase from 2 to 6 weeks, nor does the proportion of carrying episodes terminated in this way increase (figure 4.19). Caregivers therefore become less likely to accept or take on infants as the infants get older, but either tolerate or are unable to remove infants who have succeeded in getting on. Figures 4.23 and 4.24 show that the number of unsuccessful rub-offs decreases and the percentage

Table 4.11

Spearman rank order correlation coefficients between time on caregivers and frequencies of picking up by caregivers and getting on by infants.

* $p < 0.05$. ** $p < 0.01$.

		TIME ON			
	AGE/weeks	Father	Mother	Sib 1	Sib 2
GETTING ON	2	-0.76 *	-0.33	0.45	0.07
	4	0.55	0.25	0.31	0.25
	6	0.53	0.42	0.07	0.71 *
PICKING UP	2	0.02	0.83 **	0.71 *	0.66 *
	4	0.90 **	0.11	0.28	-0.37
	6	0.75 *	0.51	-0.23	-0.78 *

of rub-offs which are successful increases over this period, so caregivers appear to be tolerating rather than failing to remove infants who are on them.

The amount of time that infants spend on caregivers is in general inversely and significantly correlated with the relative frequency with which caregivers reject their attempts to climb on (see above and table 4.10). The number of times caregivers rub infants off does not correlate negatively with the amount of time infants spend on caregivers. infant time on caregivers thus seems to be controlled by the relative rejection rate of caregivers rather than the rate at which caregivers rub infants off, and by the number of pick-ups by caregivers for mothers and siblings at 2 weeks and for fathers at 4 and 6 weeks. The only

significant correlations between the amount of time on caregivers and the number of rub-offs by caregivers are positive, suggesting a caregiver is more likely to rub off an infant it has been carrying the longer it has been carrying it. Rub-off success increases with age (see above) so caregivers who are carrying infants are choosing to let them stay on.

The proportion of tantrums occurring with each caregiver and the total frequency of tantrums decline with age over a similar time course as time with caregivers (figures 4.1 and 4.25). This is because most tantrums were observed to be associated with caregivers' attempts to rub infants off (figure 4.23). Other tantrums at 2 and 4 weeks occur after infants have been rubbed off and appear to attract the attention of other caregivers who then pick up the infant. Once infants become mobile they can approach caregivers and attempt to climb on and no longer need to call to be picked up. This suggests that though caregivers have immediate control over the time infants spend on them, their actions are probably influenced by their infants' behaviour, so that overall control of time on is a complex interaction between the behaviour of both caregivers and infants.

Figure 4.24 shows that caregivers improve their success rate at attempts to rub infants off as infants get older. There are probably several reasons for this. Caregivers most likely become skilled at rubbing off infants as they get more experience, figure 4.30 shows that infants attempting to rub off babies from the next set of offspring are only 20% successful. Infants must become easier to remove as they grow bigger. At 2 weeks they cling almost buried in the carrier's fur and are small enough, relative to the carrier, to crawl away from the area being rubbed against the substrate. By 6 or 10 weeks they are too large for this and a carrier can easily lever an infant off against a

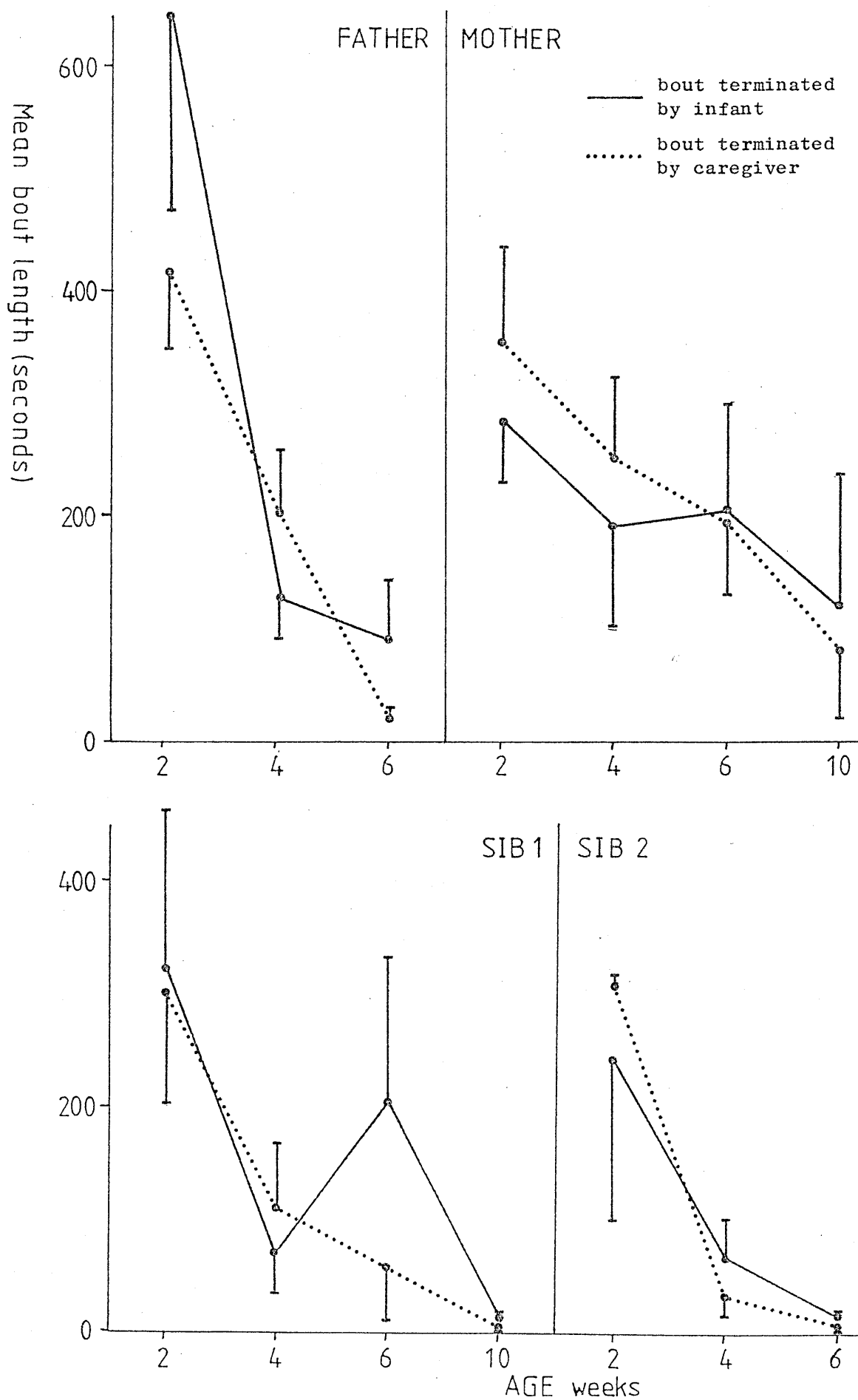
flat surface. A third possibility is that as they get older, infants are less concerned to hang on once caregivers start to try to rub them off. This would be expected from the point of view that infants are becoming more independent as they grow older and should require contact-comfort less. Harlow suggested that the growth of relationships with peers in rhesus monkey infants reduces the need for and occurrence of interactions with the mother (Harlow 1969). In the case of marmosets it may be that the growth of playful interactions with twins and siblings reduces the need for time on.

As well as the reduction in total duration, time on is spent in shorter bouts as infants get older (table 4.3). This suggests either that caregivers are removing infants sooner once on, or that infants no longer require long periods of time on and that having been on for a short while are getting off more quickly. An analysis of bout lengths of time on terminated by caregivers and by infants (figure 4.32) shows that both caregivers and infants terminate bouts sooner as infants get older, and that mean lengths of bouts ended by caregivers and by infants are not significantly different at any age. The decrease in bout length with age is therefore a consequence both of infants getting off more quickly and of caregivers rubbing them off sooner. The fact that infants are getting off after shorter bouts of time on is in line with the suggestion made above that infants are requiring less time on as they get older and may contribute to the increase in rub-off success experienced by caregivers..

Mothers have a lower relative rejection rate than other caregivers from 6 weeks onwards (figure 4.21), the difference being significant at 14 weeks. Infants try to climb on and succeed in climbing on to mothers significantly more often than on to other caregivers at 6 and 10 weeks (figure 4.19). Both explain why there is an increasing tendency with age for the caregiver who carries the infant to be the

Figure 4.32

Mean lengths of bouts of time on different caregivers terminated by infants and by caregivers. Vertical bars denote standard errors.



mother. Infants' greater persistence in trying to climb on to mothers is likely to be due to the lower rejection rate of mothers, rather than the other way round, because the number of attempts to climb on to mothers does not correlate significantly with time spent on mothers (table 4.11), whereas the amount of time 6 week old infants spend on mothers correlates inversely with the mothers rejection rates (table 4.10). Mothers' lower rejection rates are likely to be due to their still producing milk to feed their infants.

ii) The increase in time in contact with mothers from 6 weeks

As time on mothers declines, infants tend to spend more time in contact with them (figures 4.2 and 4.6). Contact with mothers allows infants to nurse and infants would be expected to maintain contact after mothers cease carrying them for this reason. This appears to be the case as the frequency of approaches to mothers by infants is significantly correlated with time in contact with mothers at 14 weeks ($r_s = 0.69$, $p < 0.05$), though not at 10 weeks.

To clarify whether or not approaches by infants do make a significant contribution to the increase of time in contact with mothers, an analysis was made of the initiation of bouts of time in contact with mothers. Where a bout of contact with the mother is preceded by an approach (to mother by infant, or to infant by mother) with no intervening changes in behaviour state, it can be calculated what proportion of these periods of contact were initiated by (by approaching) mothers and what proportion by infants. This does not account for all periods of contact since an animal can move from being on or in a family huddle to being in contact without any approach being recorded, if there was no locomotion of 20 cms or more. For example, if all participants of a family huddle moved off leaving two behind, those two would then be in contact with each other without either having approached the other.

However it does account for bouts of contact initiated from a distance provided the contact occurs soon after the approach. Data were collected for approaches that were followed by contact within 5 seconds (the majority occurred within 1 second). Figure 4.33 shows that at both 10 and 14 weeks infants initiated more bouts of contact with mothers than mothers did, the difference between mothers and infants being significant at both ages.

iii) The relative increase in time with twins after 6 weeks and the development of play

Because twins do not carry infants like parents and siblings, and very little grooming occurs between infants and twins, time with twins is made up almost entirely of time in contact and time playing. The increased time with twin, relative to time with others, between 4 and 10 weeks (figure 4.1) depends as noted above at least partly on rejections by fathers and mothers. Infants with more rejecting parents tend to spend more time with their twins (rejections by parents and time with twins being positively correlated, see table 4.9). Rejections by siblings do not have this effect. However, the frequencies of approaching and leaving by siblings are significantly correlated with time spent with twin (table 4.12). Infants spend more time with twins when siblings are approaching and leaving them more. Approaching between infants and twins is not correlated with time with twins.

After 10 weeks time with twin declines, this is mainly due to a decrease in contact as play continues to occur at a relatively high level. As would be expected, both infant and twin leave each other equally often (figure 4.17) and come to spend more time apart (figure 4.11). As infants get older and become more independent they spend more time alone exploring and manipulating the cage (figure 4.10). They also spend more time playing with siblings, and time playing with sibs and time in

Figure 4.33

Initiation of contact with mothers: Mean frequency of approaches by infants and by mothers that are followed by contact with mothers within 5 seconds.

Dotted bars denote approaches by infants. Open bars denote approaches by mothers. Vertical bars denote standard errors.

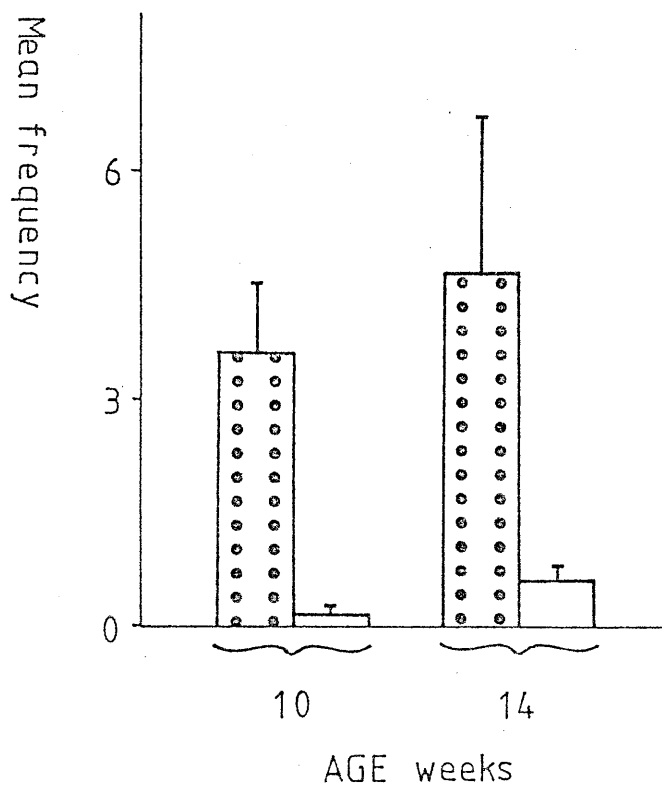


Table 4.12

Spearman rank order correlation coefficients between frequencies of various behaviours and durations of time with twin, and time playing with siblings and twin. Mean scores of the behaviours (frequency or duration) are correlated over time, i.e. 2 to 22 weeks.

* $p < 0.05$. ** $p < 0.01$. @ correlated over 10 to 22 weeks.

FREQUENCY OF:	DURATION OF:		
	Time with twin	Play with siblings	Play with twin
Siblings leave infant	0.77 **		
Siblings approach infant	0.50 *	-0.17	
Infant approaches siblings		0.76 **	
Infant approaches twin	0.35		0.80 *
Twin approaches infant	0.42		0.73 *
Siblings ignore infant		-0.08 @	

contact with twins are significantly negatively correlated ($r_s = -0.81$, $p < 0.01$).

Play develops from 4 weeks and occurs mainly with the twin (figure 4.8). Time spent playing with twins is significantly correlated with both approaches by infants and approaches by twins (table 4.12), suggesting both infant and twin contribute to the maintenance of play with each other (expected, since twins are infants).

Play also occurs with siblings from 4 weeks and reaches a peak at 14 weeks. Though the amount of play with siblings is small in absolute terms when compared with that with twins, it is very noticeable as almost all infants' time with siblings from 10 weeks is spent playing with them (figure 4.9), and play with siblings is often more vigorous and noisy than play with twins.

Frequencies of approaching by infants and siblings are in general not significantly different from each other after 6 weeks (figures 4.15 and 4.16). However numbers of approaches by siblings remain at the same level or decrease with time, while numbers of approaches by infants increase with time. Thus the increase in play with siblings seems to be due to the increase in approaches by infants. Time playing with siblings is significantly correlated with frequency of approaches by infants, but not with approaches by siblings (table 4.12). Infants appear to be the immediate cause of the increase in play with siblings with time, at least in the case of close-proximity play (wrestling, biting and hitting). Chasing play can be initiated over a distance. Animals will look at each other in a tense attitude across the cage, one may bob up and down and the other then suddenly race across to it and a chase ensues. Responsibility for the initiation of play from a distance cannot be determined from the present data.

The frequency of ignores by siblings declines from 10 weeks

(figure 4.26), this is in line with the suggestion made above that it is infants that initiate play with siblings as it could be interpreted as infants becoming more successful at getting siblings' attention (since ignores by siblings decline). However, ignoring and playing are not significantly inversely correlated (table 4.12).

The analysis presented above suggests that infant time on caregivers is controlled primarily by the caregivers' tendency to reject, and that when rejected by a parent the infant tends to spend its time with its twin. Siblings are relatively unimportant as carriers of infants but appear later as play partners on the initiative of the infants. Twins are important at all ages, first for contact and later for play, and appear to act as companions or 'standby caregivers' for situations when the parents are no longer available, and before infants are ready to take on playful interactions with the siblings.

b) The effect of handling on caregiving behaviour

As noted in chapter 2, one older sibling of each infant had been the infant subject of the previous litter and had thus been caught, marked with picric acid and weighed at fortnightly intervals for the first eight weeks of life. A re-examination of the data presented in sections 4.2) to 4.4) shows whether this minimal amount of handling had any effect on the caregiving behaviour of these siblings. Table 4.13 gives the results of randomization tests between pairs of siblings (sib 1's and sib 2's) for all behaviours recorded at each age.

With 127 tests being carried out and a 5% significance level, six tests could be expected to be significant by chance. In fact 15 tests gave a significant result (11.8% of the total) but there is no consistent pattern to the differences, siblings alternating as to which has the greater score for any particular behaviour.

Table 4.13

Results of two-tailed randomization tests between pairs of siblings (sib 1's and sib 2's) for various behaviours.
 * significant difference between siblings ($p < 0.05$). ns not significant. - not applicable.

BEHAVIOUR	FIGURE	AGE/weeks						
		2	4	6	10	14	18	22
Mean time with	4.1	ns	*	*	ns	ns	ns	ns
Mean time on	4.2	ns	ns	ns	*	ns	ns	ns
Mean time on as percentage total time on	4.3	ns	ns	ns	*	ns	-	-
Mean time siblings grooming infant	4.4	ns	ns	ns	*	ns	ns	ns
Mean time infant grooming siblings	4.5	ns	*	*	ns	ns	ns	ns
Mean time in contact	4.6	ns	ns	ns	ns	ns	ns	ns
Mean time playing	4.8	ns	ns	ns	ns	ns	ns	ns
Mean proportion of time with playing	4.9	ns	ns	ns	ns	*	ns	ns
Mean frequency of sibling approaches infant	4.15/16	ns	ns	ns	ns	ns	ns	ns
Mean frequency of sibling leaves infant	4.15/16	ns	*	ns	ns	ns	ns	ns
Mean frequency sibling picks up infant	4.19	ns	ns	*	ns	-	-	-
Mean frequency sibling rubs off infant	4.19	ns	*	ns	ns	-	-	-

Table 4.13 continued.

BEHAVIOUR	FIGURE	AGE/weeks						
		2	4	6	10	14	18	22
Mean frequency infant avoids carry	4.20	ns	ns	ns	-	-	-	-
Mean absolute rejection rate	4.21	ns	ns	ns	ns	ns	ns	ns
Mean relative rejection rate	4.21	ns	ns	ns	ns	ns	ns	ns
Mean frequency sibling fails to rub off	4.23	ns	ns	ns	-	-	-	-
Mean percentage rub-off success	4.24	*	ns	ns	-	-	-	-
Mean percentage tantrums with sibling	4.25	ns	ns	ns	*	*	ns	ns
Mean frequency of ignores by sibling	4.26	ns	ns	ns	ns	ns	ns	ns
Mean frequency of food-stealing attempts	4.27	ns	*	ns	ns	ns	ns	*
Mean frequency of aggressive acts	4.29	ns	ns	ns	ns	ns	ns	ns

Generally, differences in behaviour between handled and unhandled siblings are small, inconsistent and non-significant, and for the purposes of analysis a single category 'siblings' can be used to cover sib 1's and sib 2's. In later chapters data from both siblings will be combined in the presentation of results.

Differences may also occur with respect to the sex of the siblings, this will be discussed in section 4.7).

c) Caregiving changes at 10 weeks - 'baby transition'

Ingram (1975a) has suggested dividing up the marmoset lifespan into the following stages which she bases on behavioural and morphological characteristics:

Infant	0 - 12 weeks
Juvenile	12 - 24 weeks
Adolescent	24 - 40 weeks
Subadult	40 - 56 weeks
Adult	> 56 weeks

In this study therefore, subjects fall into the infant and juvenile categories. However, various behavioural measures described in the previous sections suggest another division is appropriate at about 10 weeks. This age seems to mark a change in the responsiveness of caregivers towards infants. Before 10 weeks offspring are treated as "babies", are carried most of the time, protected and indulged. After 10 weeks the infants spend most time off, interact far less with parents and expand independent activities such as playing and manipulating objects in the cage. The data which indicate this 'baby transition' have already been described above but are given again below collected together for clarity.

Both time with (figure 4.1) and time on (figure 4.2) drop off

markedly as the infant gets older, with the greatest rate of decline occurring from 2 to 10 weeks. From 10 weeks the drop in time with levels out, the exception being time with twin which does not show such a marked decrease. Infants spend most of this time with being carried from 2 to 6 weeks, but from 10 weeks very little time is spent on.

Grooming by fathers decreases sharply at 10 weeks, and continues to drop thereafter, though grooming by other caregivers drops off more slowly (figure 4.4). On the contrary, infants increase their grooming of caregivers from 10 weeks, particularly of mothers (figure 4.5).

The increase with age of time spent in family huddles shows a dip at 10 weeks (figure 4.7) and time off also shows a slight dip here (figure 4.10). The dips are filled with time in contact with caregivers, specifically an increase in the amount of time spent in contact with mothers (figure 4.6).

Total %AP.I - %LV.I (figure 4.12) peaks at 6 weeks indicating infants are most responsible for proximity with their caregivers at this age. From 10 weeks %AP.I - %LV.I drops as infants make fewer approaches to caregivers (figures 4.13 - 4.17).

Any time spent on from 10 weeks is due entirely to infants getting on, caregivers do not pick infants up from 6 weeks (figure 4.19) and consequently infants no longer avoid being carried (figure 4.20). Relative rejections, except by mothers, reach a plateau at 10 weeks (figure 4.21), though absolute rejections decline due to the decreased frequency of attempts by infants to get on. Caregivers do not restrict infants' attempts to get off after 6 weeks (figure 4.22).

The frequency of ignores by fathers and by siblings peak at 10 weeks, while those by mothers peak at 6 weeks and remain at a high level at 10 weeks (figure 4.26). The frequency of food-stealing attempts by

infants from mothers and siblings is highest at 10 weeks (figure 4.27) but success at food-stealing shows a marked drop at this age (figure 4.28). Mothers show most aggression towards infants at 10 weeks, siblings most at 6 weeks.

The data all point to a change in the way caregivers behave towards infants occurring over the period from 6 to 10 weeks of age. Before this time infants spend a lot of time on and with caregivers, are groomed, may be restricted in their efforts to get off and are allowed to food-steal. At 10 weeks this changes, caregivers become more aggressive and rejecting, and ignore infants. Infants try to maintain the attention of caregivers as shown by the more positive %AP.I - %LV.I and increased grooming, but then adjust to the altered level of caregiving by spending most time off, increasing play (with siblings) and exploring on their own. The exception to these changes is in infants' relations with their twins, which show no marked 'baby transition'. This is presumably because the twins are themselves going through the same stage of adjustment. This may explain why infants with rejecting parents turn to twins to spend time with, the twin is also experiencing the rejections and has similar requirements for contact-comfort and attention.

d) Behaviour meshing and compensation

This section deals with whether or not caregivers compensate for differences in each others' caregiving behaviour, and whether or not infants' and caregivers' behaviour becomes meshed with respect to each other.

i) Compensation

Compensation is said to occur when one class of caregiver performs correspondingly more of a behaviour than another class of

caregiver performs less of. Parents and siblings do not generally compensate for each others' behaviour towards infants, but twins do appear to do so.

Time on fathers, on mothers and on siblings are not significantly negatively correlated at 2, 4 or 6 weeks (table 4.14), though time on fathers is inversely correlated with time with twins at 4 and 6 weeks (table 4.15). Infants who are rejected a lot by one caregiver or who spend little time on one caregiver do not make a correspondingly large number of attempts to climb on to other caregivers (table 4.17), instead, infants with rejecting parents spend more time with twins (table 4.9).

Infants with highly rejecting fathers do not have unrejecting mothers or siblings, and vice versa. On the contrary, infants with rejecting fathers tend to have rejecting mothers and siblings as well. Similarly, infants with tolerant fathers, i.e. those that allow infants to climb on to them more often, tend to have tolerant mothers and siblings as well (table 4.14).

There is no consistent pattern between time on caregivers and time in contact with mothers (table 4.16). Infants who spend little time on fathers and siblings at 4 weeks tend to spend more time in contact with mothers, but at 6 weeks there is a positive correlation between time on mothers and time in contact with mothers. Mothers do not therefore compensate for small amounts of time carrying infants by an increased amount of time in contact with them.

Infant subject number 2 had only one sibling and subject number 8 was without a twin, each therefore had one less play partner than the other seven infants. If the remaining two play partners compensate for this loss by playing with the infant more, the total time spent playing by these infants should be no less than that by the rest. Although the sample is too small for any statistical analysis, the direction of

Table 4.14

Spearman rank order correlation coefficients for mother-infant versus father-infant behaviour, mother-infant versus sibling-infant behaviour, and father-infant versus sibling-infant behaviour.

* $p < 0.05$. ** $p < 0.01$.

BEHAVIOUR	AGE/ weeks	CAREGIVERS		
		Mother vs father	Mother vs siblings	Father vs siblings
Time on caregiver	2	-0.38	-0.54	-0.31
	4	-0.55	-0.12	0.62 *
	6	0.74 *	0.33	0.24
Absolute frequency of rejections by caregiver	4	0.75 *	0.60	0.35
	6	0.26	0.33	0.33
Relative frequency of rejections by caregiver	4	0.55	0.23	0.73 *
	6	0.68 *	0.40	0.04
Number of times infants climb on to caregivers	2	0.38	0.59 *	0.60 *
	4	0.16	-0.03	0.64 **
	6	0.64 *	0.33	0.47 *

Table 4.15

Spearman rank order correlation coefficients between time spent by infants on caregivers and time spent with twins.

* $p < 0.05$. ** $p < 0.01$.

TIME WITH TWIN VS TIME ON:	AGE/weeks		
	2	4	6
Father	0.18	-0.85 **	-0.82 *
Mother	0.43	0.40	-0.53
Siblings	0.43	-0.54	0.10

Table 4.16

Spearman rank order correlation coefficients between time spent by infants on caregivers and time in contact with mothers.

* $p < 0.05$. ** $p < 0.01$.

CONTACT WITH MOTHERS VS TIME ON:	AGE/weeks	
	4	6
Father	-0.96 **	0.48
Mother	-0.23	0.79 *
Siblings	-0.68 *	0.32

Table 4.17

Spearman rank order correlation coefficients between various measures of behaviour and the number of attempts that infants make to climb on to other caregivers. Upper figure of each pair refers to 4 week old infants, lower to 6 week olds.

* $p < 0.05$. ** $p < 0.01$.

BEHAVIOUR	NO. ATTEMPTS TO CLIMB ON TO OTHERS
Time on mother	-4.2 x 10 ⁻³ 0.19
Time on father	-0.15 0.19
Time on siblings	0.17 0.32
Absolute frequency of rejections by mother	-0.05 -0.10
Absolute frequency of rejections by father	0.13 0.42
Absolute frequency of rejections by siblings	0.22 -0.48
Relative frequency of rejections by mother	-0.11 -0.10
Relative frequency of rejections by father	4.2 x 10 ⁻³ -0.33
Relative frequency of rejections by siblings	-0.22 -0.58

differences in time spent playing by infant subjects may suggest whether compensation is occurring. Table 4.18 shows how many of the other seven infant subjects played more than the two with one less play partner. Subject number 8 played less than most other infants at most ages, suggesting that its sibling did not make up for loss of a twin in time playing. However by 22 weeks subject number 8 is no different from the rest (playing less than 3 out of 7). Conversely, subject number 2 plays more than most other infants from 6 to 18 weeks, indicating loss of its sibling did not cause a reduction in total time spent playing. This may be partly due to the relatively small amount of time siblings spend playing with infants in the early weeks (figure 4.8), but could also be due to compensation by the remaining sibling and by the twin. As the siblings of subject number 8 did not compensate for loss of twin, it is likely that any compensation for loss of sibling is due to the twin rather than the other sibling. Alternatively, subject number 2 may be an exceptionally playful infant. A much larger sample is needed for firm conclusions.

Hence it would appear that fathers, mothers and siblings do not compensate for each other in the amount of time they carry infants, in how rejecting or how tolerant they are. Twins compensate by spending more time with infants who have rejecting parents and who spend little time on fathers, and may perhaps compensate for siblings who play little.

ii) Meshing

Meshing, as described by Hinde and Simpson (1975), is the degree to which the behaviour of two animals fits together, that is, how far the goals of each are aligned. Meshing between mother and infant rhesus monkeys has been shown to improve with age (Hinde & Simpson, 1975; Hinde & White, 1974) and can be regarded as a measure of socialization. As an animal becomes more socialized so its behaviour fits in better with that of the other animals in its social group.

Table 4.18

Differences in total time spent playing between subject numbers 2 and 8 and the other seven infants. Figures give number of other infants (out of seven) compared with which subject numbers 2 and 8 spent less time playing.

INFANT SUBJECT	AGE/weeks					
	4	6	10	14	18	22
2	6	2	2	1	0	4
8	7	7	7	6	5	3

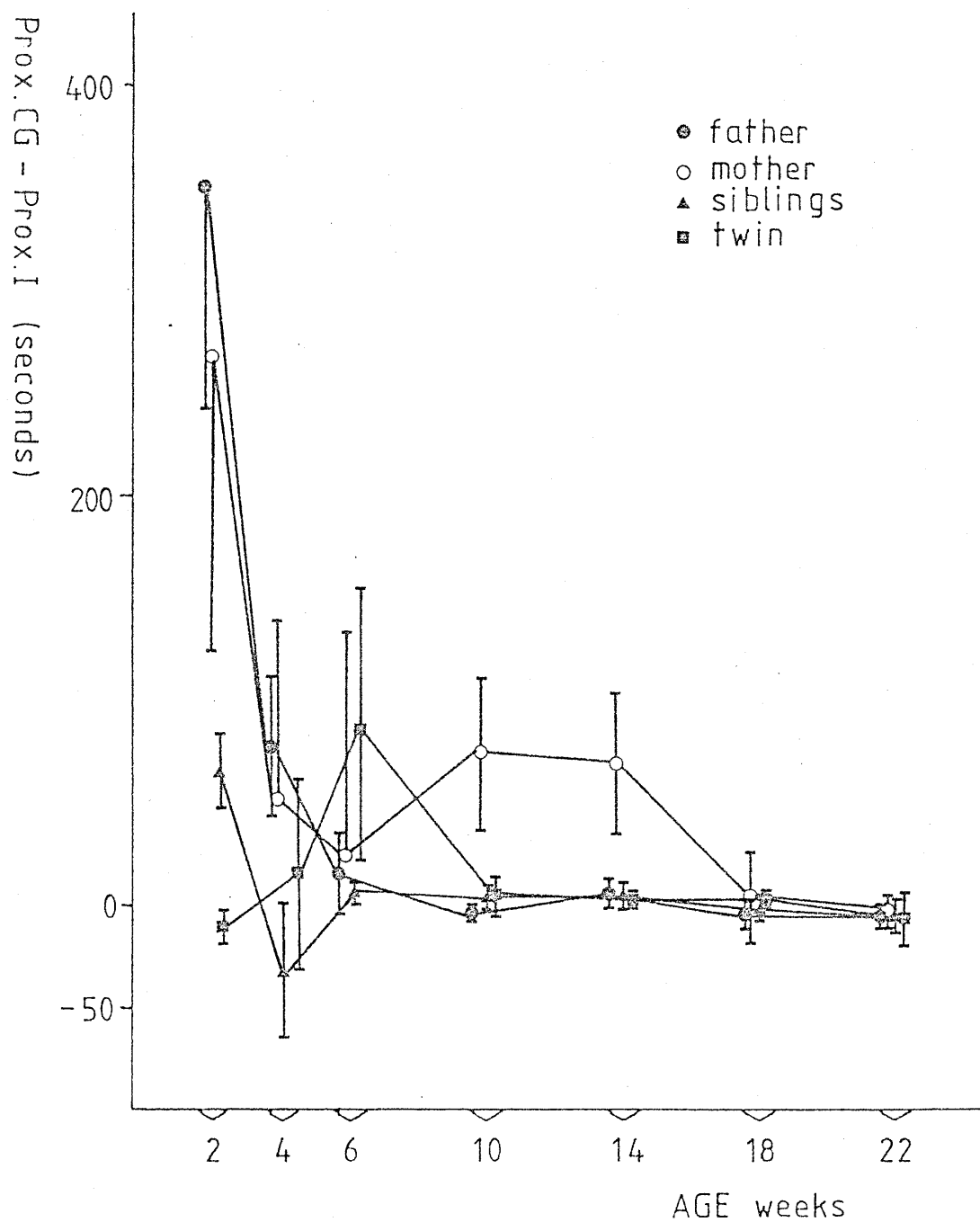
One indication of meshing is the fact that the absolute rejection rate falls while the relative rejection rate remains high (figure 4.21). This shows that while caregivers continue to reject a high proportion of infants' attempts to get on, infants become less likely to make such attempts.

Hinde looked at meshing by measuring the changes in probability that bouts of ventral-ventral contact would be terminated by mother or infant during successive intervals after initiation of contact. Another method is to see how well bout lengths of time with terminated by caregivers and by infants correspond. Figure 4.34 shows the index $\text{Prox.CG} - \text{Prox.I}$ for each caregiver. The index consists of the mean length of bouts of proximity terminated by the caregiver minus the mean length of bouts of proximity terminated by the infant. The term 'proximity' is used here instead of time with as individual bouts are measured as the time between an approach (by caregiver or infant) and the next leaving recorded

Figure 4.34

Proximity maintenance, Prox.CG - Prox.I. Mean bout length of episodes of proximity terminated by caregivers minus mean bout length of episodes of proximity terminated by infants.

Conventions as in figure 4.1.



between them. (Time with is total time spent on, in contact, grooming and playing with a caregiver).

Figure 4.34 shows that for all caregivers except the mother Prox.CG - Prox.I is near to zero by 10 weeks of age and remains at this level. A score of zero indicates infants and caregivers are leaving each other on average after the same length of time since approaching each other. Hence by 10 weeks infants are well meshed with fathers, siblings and twins. Proximity with mothers is not so well meshed until 18 weeks of age. Before this, Prox.CG - Prox.I is more positive indicating mothers tend to leave after longer bouts than do infants. Observations showed that long bouts of proximity with mothers at these ages usually occurred when the infant was nursing, and that mothers normally ended feeding sessions by walking away from their infants.

Before 10 weeks Prox.CG - Prox.I is generally more positive for all caregivers. This suggests that from 2 to 6 weeks caregivers provide as much proximity as the infant needs, since infants tend to leave sooner than caregivers. The fact that the measure reaches near zero for most caregivers by 10 weeks is in line with other data presented in section c) above which suggested a 'baby transition' at this age.

Scores for twins tend to be nearest zero at all ages, and scores for siblings nearer zero than scores for parents. This suggests that meshing may be a function of the age or category of the partner as well as the age of the infant.

The results from this measure are in agreement with the work by Hinde and indicate that infant marmosets do indeed become better meshed with their caregivers as they get older. Meshing could improve by infants becoming more responsive to behavioural signals from caregivers, or by caregivers becoming more responsive to signals from infants. Ainsworth et al (1974) suggest socialization in human infants is a product of

reciprocal responsiveness to signals. Babies who cried less by the end of their first year were those whose mothers had been most attentive to them. However, the precise mechanisms behind the improvement in meshing with age (i.e. socialization) require further work and an experimental approach for their elucidation.

4.6) CONSEQUENCES OF INTERACTIONS

The aim of this section is to investigate interactions between caregivers and infants further by looking at particular behaviours and what tends to follow them. The consequences of two important infant-caregiver interactions are examined: what happens to infants after they have been rubbed off by caregivers, and what happens after they have been rejected. The data are presented in two ways. Firstly by caregiver; that is, which individuals do infants tend to interact with next after a rub-off or rejection? And secondly by behaviour; that is, what types of interaction (if any) tend to follow rub-offs and rejections? Further partitioning of the data into which individuals perform which behaviours with infants after rub-offs or rejections was not possible as there are insufficient data. For ease of comparison results are given as the proportions of consequences falling into each category. The original frequencies may be found in figures 4.19 (for numbers of rub-offs by each caregiver) and 4.21 (for numbers of rejections) and are also shown in figures 4.35 to 4.38. Statistical comparisons between proportions are again made by two-tailed randomization tests.

a) Consequences of rejections

If time spent on caregivers depends on the rate of rejections by the caregivers as suggested in section 4.5), how 'rejecting' an individual

is becomes important. A more rejecting parent may be one that rejects more often, and/or one that rejects more effectively. How effectively a caregiver rejects could be measured by the time elapsing between a rejection and the next attempt by the infant to get on that caregiver. However the situation is complicated by the presence of other caregivers. Another individual may pick up an infant and thus interfere with the infant's response to the caregiver which rejected it.

To overcome this problem 'rejectingness' is examined by looking at the immediate effects of rejections - what happens next? Data are given for rejections by parents and siblings at 4 and 6 weeks, and additionally, at 10 and 14 weeks for mothers only due to the infrequent occurrence of rejections by other caregivers after 6 weeks (figure 4.21).

i) Which caregiver does a rejected infant interact with next?

Figure 4.35 shows what proportion of rejections by each caregiver were followed by interactions with each caregiver and what proportion by no interaction. For these purposes, an interaction was scored as the next caregiver to approach or be approached by the infant within 30 seconds of the rejection. If no social behaviour was recorded within 30 seconds the rejection was designated as being followed by no interaction. The significance of differences between the proportion of rejections followed by interactions with different caregivers are given in table 4.19.

At 4 weeks of age, rejections by fathers are most often followed by interactions with siblings and by no interaction. Rejections by mothers are most often followed by interactions with mothers and by no interactions. Rejections by siblings are most often followed by interactions with siblings, but also by interactions with twins and by no interactions.

At 6 weeks of age, rejections by fathers are generally not

Figure 4.35

Consequences of rejections by different caregivers. i) Who next?

Graphs show proportions of interactions with each caregiver following rejections by different caregivers. Figures give mean number of rejections (\pm standard error) by that caregiver at each age.

● Father. ○ Mother. ▲ Siblings. ■ Twin. × No-one (no interaction).

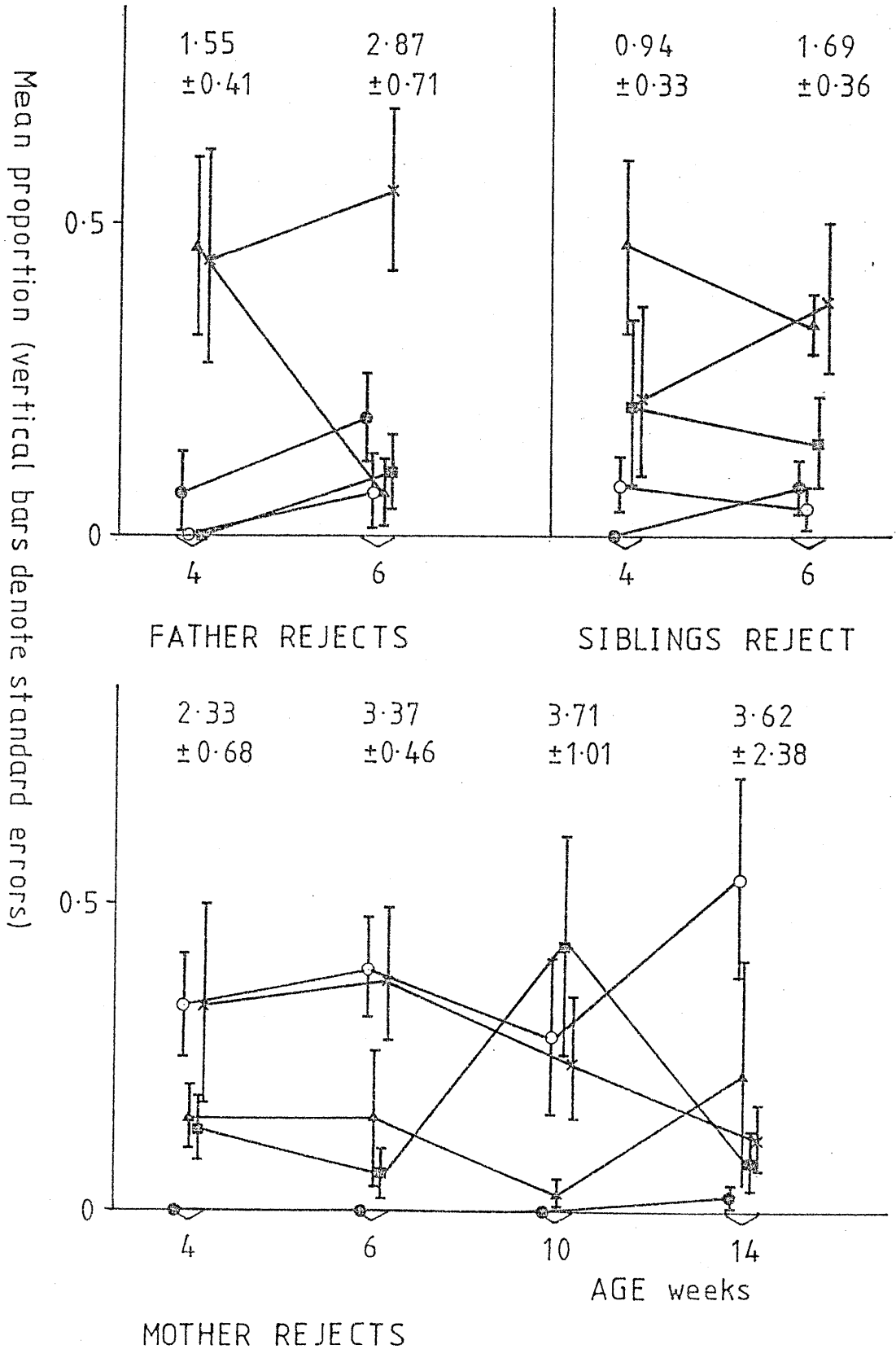


Table 4.19

Two-tailed randomization tests between proportions of consequences of rejections falling into different categories of who the infant interacts with next, that is, father, mother, siblings, twin or no-one (i.e. no interaction within 30 seconds).

> higher proportion with first caregiver in lefthand column. < higher proportion with second caregiver. * significant difference at 5% level. ns not significant. - not applicable.

CAREGIVERS	AGE/weeks			
	4	6	10	14
Consequences Of Rejections By Fathers				
Siblings vs father	* >	ns		
No-one vs father	* >	* >		
Father vs twin	ns	ns		
Father vs mother	-	ns		
Twin vs mother	-	* >		
Siblings vs no-one	ns	* <		
Consequences Of Rejections By Mothers				
Mother vs siblings	* >	ns	-	ns
Mother vs twin	* >	ns	ns	* >
No-one vs siblings	ns	ns	* >	ns
No-one vs twin	ns	ns	ns	ns
Siblings vs twin	ns	ns	ns	ns
Mother vs no-one	ns	ns	ns	* >
Father vs twin	-	-	-	* <
Father vs no-one	-	-	-	* <
Father vs siblings	-	-	-	* <
Mother vs father	-	-	-	* >
Consequences Of Rejections By Siblings				
Siblings vs no-one	ns	ns		
Siblings vs twin	ns	* >		
Siblings vs mother	* >	* >		
Twin vs mother	ns	ns		
No-one vs twin	ns	* >		
Twin vs father	-	ns		
Father vs mother	-	* >		

10
followed by interactions. Rejections by mothers are least likely to be followed by interactions with fathers. Rejections by siblings are most likely to be followed by interactions with siblings or by no interaction.

Rejections by mothers at 10 weeks lead most often to interactions with mothers or twins or to no interaction. At 14 weeks interactions following rejections by mothers occur most often with mothers and least often with fathers. (For details see figure 4.35 and table 4.19.)

General conclusions which may be drawn from these data are as follows:

- 1) Rejections are at least equally likely to be followed by no interaction as by interaction with a caregiver.
- 2) Interactions following rejections are frequently with the caregiver which was responsible for the rejection, though this is not apparent in the case of rejections by fathers.
- 3) There are no clear trends with increasing age of infants, rejections by caregivers at one age tend to have the same immediate effects as rejections by those caregivers at another age.
- 4) Rejections by caregivers tend not to be followed by interactions with fathers, and this is specifically so in the case of rejections by mothers.

ii) Which interactions occur next with a rejected infant?

An examination of the recordings of behaviour showed that after being rejected, infants may either be carried again, may come into contact with a caregiver, may play or may remain off and away from caregivers.

The interactions with caregivers begin with an approach between the caregiver and the infant. As in section i) above, a rejection is followed by no interaction when none of the other categories listed above occurs within 30 seconds of the rejection. In practice, responses

to rejections usually occur within 5 seconds. If no interaction occurs for 30 seconds it is likely that the infant will continue to spend several minutes on its own before next interacting with another individual. Thus seven immediate consequences of rejections were found to occur, though others, such as grooming, are possible. The seven are: Infant approaches a caregiver, a caregiver approaches infant, infant gets on a caregiver, a caregiver picks up infant, infant comes into contact with a caregiver, infant plays with a caregiver, and no interaction. Figure 4.36 shows what proportion of rejections by caregivers were followed by each of these behaviour categories. Table 4.20 shows where differences between these proportions are significant.

At 4 weeks, rejections by fathers are equally likely to be followed by approaches by infants, by approaches by caregivers, and by no interaction. Other interactions are much less likely. The same consequences occur after rejections by siblings. Rejections by mothers are most often followed by infant approaches and by no interaction.

At 6 weeks, rejections by fathers are again most likely to be followed by approaches by infants or by caregivers, or by no interaction, and much less likely to be followed by other interaction. Rejections by siblings are also more likely to be followed by approaches or by no interaction than by other behaviours, but infants are more likely to approach caregivers than caregivers are to approach infants. Rejections by mothers are most likely to be followed by infant approaches.

Consequences of rejections by mothers at 10 and 14 weeks are similar. Infants are not carried but rejections may be followed by any of the other behaviours. (For details see figure 4.36 and table 4.20.)

In general, rejections by caregivers appear to be effective in preventing further interaction other than approaches. Consequences of rejections depend partly on which caregiver is rejecting: For fathers

Figure 4.36

Consequences of rejections by different caregivers. ii) What next?

Graphs show proportions of different sorts of interaction following rejections by different caregivers. Figures give mean number of rejections (\pm standard error) by that caregiver at each age.

● infant approaches caregiver. ○ caregiver approaches infant. ▲ infant gets on. △ infant is picked up. ■ contact. □ play. × no interaction.

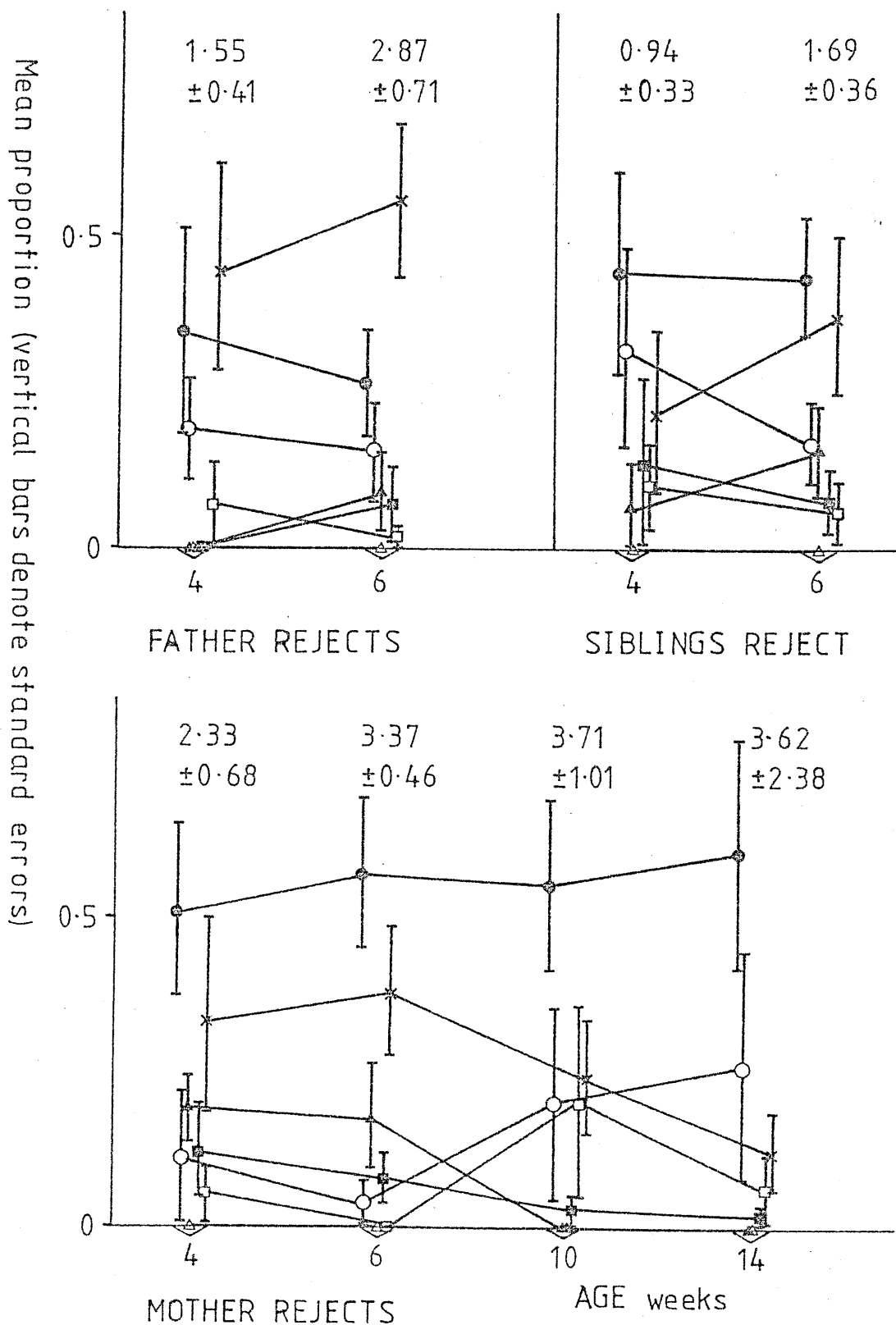


Table 4.20

Two-tailed randomization tests between proportions of consequences of rejections falling into different categories of interactions which occur next. For full names of categories see text or figure 4.36.

> higher proportion with first category in lefthand column. < higher proportion with second category. * significant difference at 5% level. ns not significant.

INTERACTIONS	AGE/weeks			
	4	6	10	14
Consequences Of Rejections By Fathers				
None vs inf. app.	ns	ns		
Inf. app. vs CG. app.	ns	ns		
None vs CG. app.	ns	ns		
Inf. app. vs play	* >	* >		
CG. app. vs play	* >	* >		
None vs contact	* >	* >		
None vs play	* >	* >		
Consequences Of Rejections By Mothers				
Inf. app. vs none	ns	* >	ns	* >
None vs inf. gets on	ns	ns	* >	* >
None vs contact	ns	* >	* >	ns
None vs CG. app.	ns	* >	ns	ns
Inf. gets on vs play	* >	* >	* <	ns
Inf. gets on vs contact	* >	ns	* <	* <
Inf. app. vs CG. app.	* >	* >	ns	ns
Contact vs play	ns	* >	ns	ns
None vs play	* >	* >	ns	* >
Consequences Of Rejections By Siblings				
Inf. app. vs CG. app.	ns	* >		
Inf. app. vs none	ns	ns		
CG. app. vs none	ns	ns		
Inf. app. vs contact	ns	* >		
CG. app. vs contact	* >	* >		
Inf. gets on vs contact	ns	ns		
None vs inf. gets on	ns	ns		
None vs contact	* >	ns		
CG. app. vs play	* >	ns		

and siblings rejections are generally equally likely to be followed by approaches by infants, approaches by caregivers, or no interaction. In the case of mothers, rejections are more likely to be followed by infants approaching than caregivers approaching or no interaction. Consequences of rejections by caregivers are the same at 4 weeks as at 6 weeks, but rejections by mothers at 10 and 14 weeks have different consequences in that no one behaviour is particularly likely to occur.

b) Consequences of rub-offs

The same behaviour categories were scored for consequences of rub-offs as for consequences of rejections above. Data are given for rub-offs at 2, 4 and 6 weeks of age only as the behaviour occurs very infrequently after this.

i) Which caregiver does a rubbed off infant interact with next?

Figure 4.37 shows what proportions of rub-offs by each caregiver were followed by interactions with each caregiver and what proportion by no interaction. Table 4.21 shows where differences between these proportions were significant.

At 2 weeks of age, rub-offs by fathers are followed most often by interactions with siblings and mothers. Rub-offs by mothers are most often followed by interactions with fathers. There are no significant differences between the proportions of rub-offs by siblings followed by interactions with fathers, mothers or siblings, but all of these are significantly more likely than interactions by the infants with their twins.

At 4 weeks of age, rub-offs by fathers may be followed by interactions with any caregiver. Rub-offs by mothers are most likely to be followed by interactions with fathers. Rub-offs by siblings are unlikely to be followed by interactions with caregivers as no interaction

Figure 4.37

Consequences of rub-offs by different caregivers. i) Who next?

Graphs show proportion of interactions with each caregiver following rub-offs by different caregivers. Figures give mean number of rub-offs (+ standard error) by that caregiver at each age.

● Father. ○ Mother. ▲ Siblings. ■ Twin. × No-one (no interaction).

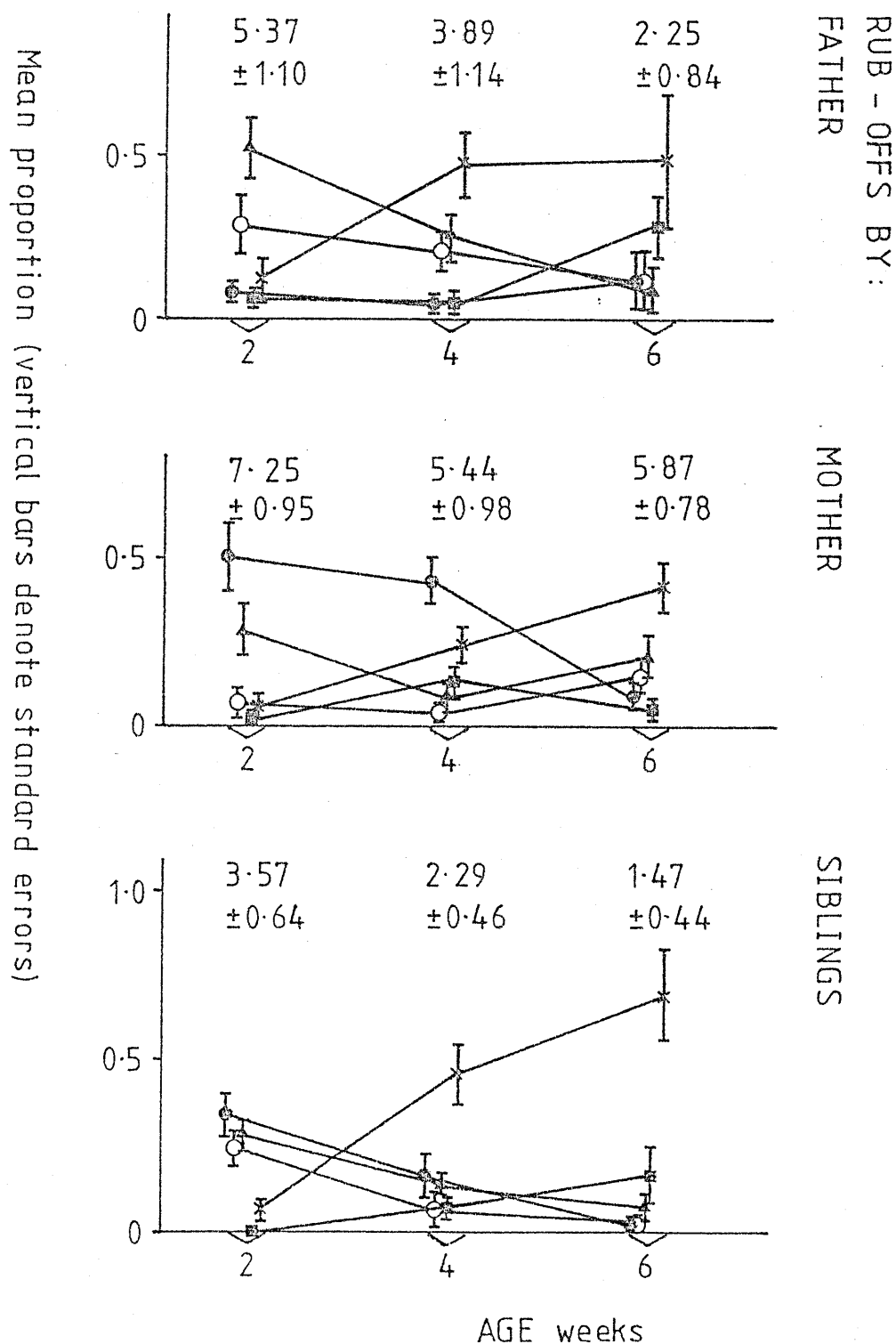


Table 4.21

Two-tailed randomization tests between proportions of consequences of rub-offs falling into different categories of who the infant interacts with next, that is, father, mother, siblings, twin or no-one (i.e. no interaction within 30 seconds).

> higher proportion with first caregiver in lefthand column. < higher proportion with second caregiver. * significant difference at 5% level. ns not significant.

CAREGIVERS	AGE/weeks		
	2	4	6
Consequences Of Rub-offs By Fathers			
Siblings vs mother	ns	ns	ns
Mother vs no-one	ns	ns	* <
No-one vs siblings	* <	ns	* >
Mother vs twin	* >	ns	* <
No-one vs twin	ns	* >	ns
Twin vs siblings	* <	ns	ns
Twin vs father	ns	ns	* >
Siblings vs father	* >	ns	ns
Mother vs father	ns	ns	ns
Consequences Of Rub-offs By Mothers			
Father vs siblings	ns	ns	ns
Mother vs siblings	ns	ns	ns
Father vs no-one	* >	ns	ns
No-one vs twin	ns	ns	* >
No-one vs siblings	ns	ns	ns
Siblings vs twin	ns	ns	ns
Father vs mother	* >	* >	ns
Father vs twin	* >	ns	ns
Consequences Of Rub-offs By Siblings			
Father vs siblings	ns	ns	* <
Siblings vs no-one	* >	* <	* <
Mother vs no-one	ns	* <	* <
Father vs no-one	* >	ns	* <
Twin vs siblings	* <	ns	ns
Twin vs mother	* <	ns	* >
Twin vs father	* <	ns	* >

occurs significantly more often than any other category.

At 6 weeks of age, rub-offs by fathers tend to be followed by interactions with twins or by no interaction. Rub-offs by mothers are most likely to be followed by no interaction. Rub-offs by siblings are most likely to be followed by no interaction, and least likely to be followed by interactions with parents. (For details see figure 4.37 and table 4.21.)

General conclusions which may be drawn are:

- 1) At 2 weeks rub-offs are usually immediately followed by another interaction with a caregiver, while by 6 weeks interactions do not normally follow rub-offs.
 - 2) The interactions following rub-offs are not normally with the caregiver which rubbed the infant off.
 - 3) Parents become less frequently interacted with following rub-offs with increasing age of infants, while twins become more frequently interacted with.
 - 4) Rub-offs by fathers and siblings are not followed by interactions with particular individuals, while rub-offs by mothers at 2 and 4 weeks tend to be followed specifically by interactions with fathers.
- ii) Which interactions occur next with a rubbed off infant?

As for rejections, seven different consequences were found to follow rub-offs. The infant could 1) remain off and not interact with caregivers, 2) approach a caregiver, or 3) be approached by a caregiver. Approaches could precede 4) the infant getting on a caregiver, 5) the infant being picked up by a caregiver, 6) the infant being in contact with a caregiver, or 7) the infant playing with a caregiver. Figure 4.38 shows what proportions of rub-offs by each caregiver were followed by each of these consequences. Table 4.22 shows where differences between these proportions were significant.

Figure 4.38

Consequences of rub-offs by different caregivers. ii) What next?

Graphs show proportions of different sorts of interactions following rub-offs by different caregivers. Figures give mean number of rub-offs (\pm standard error) by that caregiver at each age.

● infant approaches caregiver. ○ caregiver approaches infant. ▲ infant gets on. △ infant is picked up. ■ contact. □ play. × no interaction.

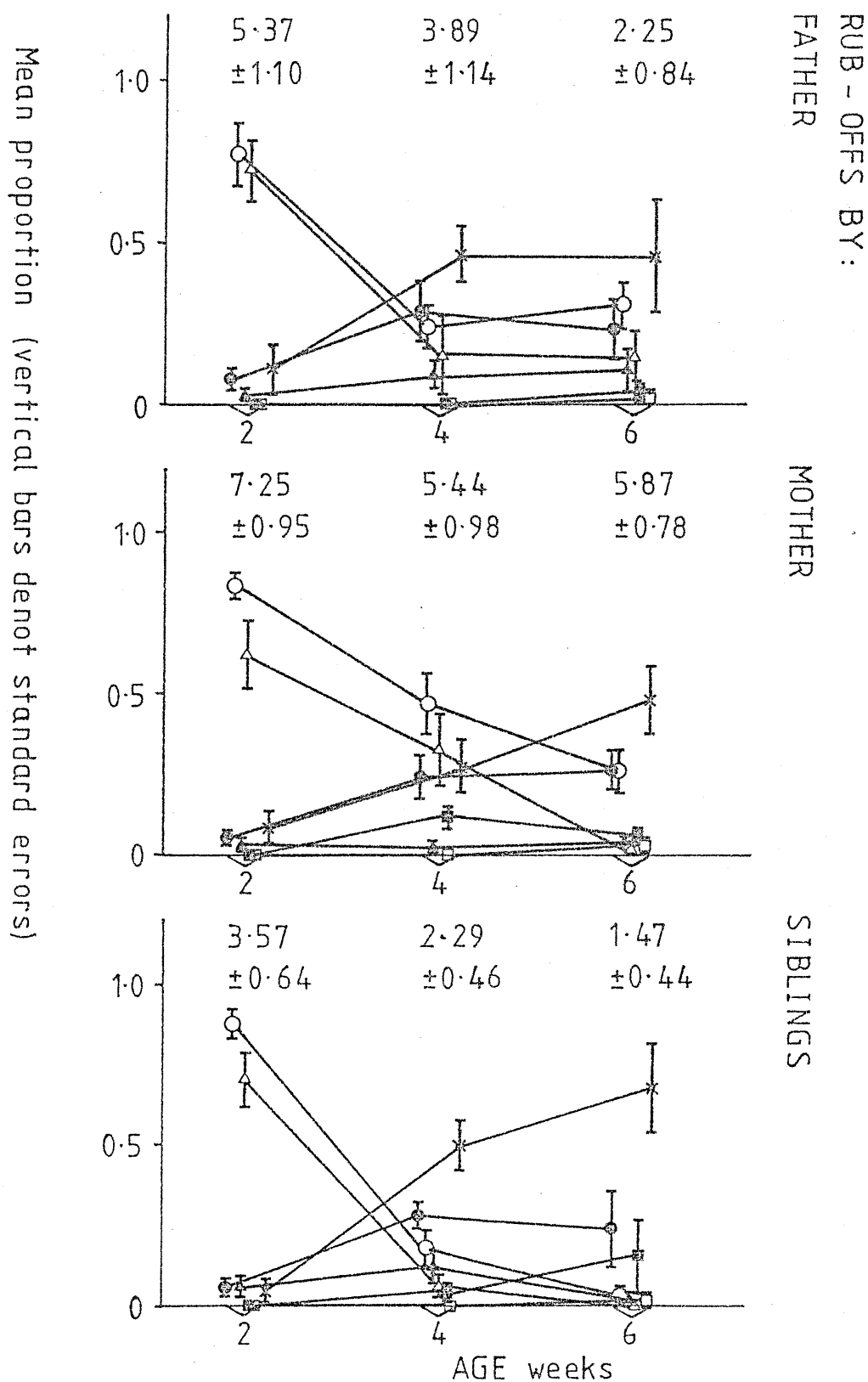


Table 4.22

Two-tailed randomization tests between proportions of consequences of rub-offs falling into different categories of interactions which occur next. For full names of categories see text or figure 4.38.

> higher proportion with first category in lefthand column. < higher proportion with second category. * significant difference at 5% level. ns not significant. - not applicable.

INTERACTIONS	AGE/weeks		
	2	4	6
Consequences Of Rub-offs By Fathers			
Inf. picked up vs none	* >	* <	ns
None vs inf. gets on	ns	* >	ns
None vs inf. app.	ns	ns	ns
None vs CG. app.	* <	ns	ns
Inf. app. vs CG. app.	* <	ns	ns
CG.app. vs inf.picked up	ns	* >	* >
CG.app. vs inf. gets on	* >	ns	* >
Inf. gets on vs play	-	-	ns
Inf. app. vs inf.gets on	ns	ns	* >
Inf.app. vs inf.picked up	* <	ns	* >
Consequences Of Rub-offs By Mothers			
CG.app. vs inf.picked up	* >	* >	* >
Inf. picked up vs none	* >	ns	* <
None vs inf. gets on	ns	* >	* >
CG. app. vs inf. app.	* >	ns	ns
CG. app. vs none	* >	ns	ns
None vs contact	-	ns	* >
Contact vs inf. gets on	-	ns	ns
CG. app. vs contact	-	* >	* >
Inf.gets on vs picked up	* <	* <	* >
Consequences Of Rub-offs By Siblings			
CG.app. vs inf.picked up	* >	* >	* >
Inf.picked up vs none	* >	* <	* <
None vs inf. app.	ns	ns	ns
Inf. app. vs CG. app.	* <	ns	ns
Inf.app. vs inf gets on	ns	* >	* >
Inf.gets on vs picked up	* <	* >	-
Inf.picked up vs contact	-	ns	ns
Inf.app. vs contact	-	* >	* >
Contact vs play	-	-	ns

At 2 weeks of age, rub-offs by fathers are most likely to be followed by caregiver approaches, and caregiver picks up infant. Rub-offs by mothers and rub-offs by siblings are also most often followed by caregiver approaches and usually by caregiver picks up infant.

At 4 weeks of age, rub-offs by fathers may be followed by no interaction, by infant approaches, or by caregiver approaches. Other interactions are less likely. Rub-offs by mothers are most often followed by caregiver approaches. Contact, play and infant gets on are least likely to occur. Rub-offs by siblings are most likely to be followed by no interaction or by infant approaches or caregiver approaches. Infant gets on is more likely than infant is picked up, contact and play.

At 6 weeks, rub-offs by fathers, mothers and siblings are all most likely to be followed by caregiver approaches, infant approaches or no interaction. (For details see figure 4.38 and table 4.22.)

In general, it makes no difference which caregiver rubs the infant off as the results are the same for all. At 2 weeks caregivers almost invariably approach and pick up a rubbed off infant. After 2 weeks this happens much less. No interaction becomes more frequent but not significantly greater than approaches by caregivers or by infants. At 4 and 6 weeks approaches occur significantly more often than the other interactions, and contact and play are particularly low.

From the above data it would appear that rejections and rub-offs differ in the consequences that follow them. This is not perhaps surprising since a rub-off follows a period of time spent on a caregiver, whereas a rejection interferes with an infant's attempt to get on.

Rub-offs tend not to be followed by interactions with the caregiver which rubbed off, whereas rejections are more likely to be

followed by interactions with the rejector. This suggests that infants do not rate caregivers equally and that caregivers may have a limit to the amount of time they are prepared to devote to infants; an infant who has been rubbed off does not attempt to interact again with that caregiver but is more likely to try someone else. An infant who has been rejected however, is likely to interact again with that caregiver, indicating that it is attempting to get on to a particular caregiver, and not just to get on. Alternatively, the infant could be trying to get on to the nearest caregiver but this would produce different results since caregivers usually leave infants after they have rejected them. The nearest caregiver would not therefore necessarily be the same one as rejected the infant. The interaction with a particular caregiver is most clear in the case of rejections by mothers (who provide milk) and a comparison of figures 4.35 and 4.36 shows that the sequence most often involved after a rejection by the mother is infant approaches mother.

Rub-offs by mothers at 2 and 4 weeks are usually followed by interactions with fathers whereas rub-offs by other caregivers are not followed by interactions with any particular caregiver. One explanation of this would be that rub-offs by mothers are more traumatic to the infant than rub-offs by other caregivers, and the infant interacts next with the caregiver which is most likely to pick it up (figure 4.19) and spend time carrying it (figure 4.2), the father.

Fathers appear to be the most effective rejectors, rejections by fathers being unlikely to be followed by further interactions with fathers. This could contribute to the very steep decline in time on fathers as compared with other caregivers (figure 4.2). Siblings are not so effective at terminating interactions by rejecting, in fact rejections are most likely to be followed by interactions with siblings, and figure

4.2 shows that the rate of decline of time on siblings is slower than that for other caregivers. This is in line with the data analysed in section 4.5) which suggested that time on caregivers is controlled mainly by rejection rates of caregivers.

4.7) SEX DIFFERENCES IN CAREGIVING BEHAVIOUR

There are three ways of looking at sex differences in infant-caregiver relationships:

- 1) Do caregivers behave differently towards male versus female offspring? Differences have previously been found for common marmosets (Ingram, 1975a & 1977), saddle-back tamarins (Cebul, 1980), hamadryas baboons (Bolwig, 1980), rhesus macaques (Mitchell, 1968b), pigtail macaques (Jensen et al, 1967 & 1968), stump-tail macaques (Estrada & Sandoval, 1977) and squirrel monkeys (Rosenblum, 1974).
- 2) Do caregivers treat infants of the same sex as themselves differently from infants of the opposite sex to themselves? This has been found to be the case in studies of bonnet macaque juveniles (Rosenblum et al, 1975).
- 3) Do male older siblings behave differently towards infants than female older siblings?

The fact that seven out of the nine infant subjects were males precludes any analysis to answer the first two questions. However the ratio of males to females among older siblings was closer to equality (ten males to six females, excluding one male singleton sibling) and this made it possible to analyse whether relationships between infants and male siblings differed from relationships between infants and female siblings. Results for male versus female siblings were compared using two-tailed Mann-Whitney U tests with a 5% significance level.

Figures 4.39 to 4.43 compare the distribution of infants' time with, time on, time in contact, grooming and playing between their male versus female older siblings. In each case the data are means of interactions by infants with a total of ten male and six female siblings.

There is wide inter-individual variability for most measures as indicated by the large standard errors, consequently few differences between the two sexes of sibling are significant.

Infants spend significantly more time with female than male siblings at 2 weeks of age (figure 4.39). This is accounted for by the difference in time on, which is also significantly higher for female than male siblings at 2 weeks (figure 4.40). Differences at other ages for time with and time on are not significant.

There are no significant differences between male and female siblings in time spent in contact with infants, or in total time spent grooming with them (time siblings spend grooming infants plus time infants spend grooming siblings). Male siblings spend significantly more time playing with infants than female siblings at 14 weeks, but differences at other ages are not significant. (See figures 4.41, 4.42 and 4.43.)

The difference in time infants spend on female and male siblings at 2 weeks of age is not accounted for by differences in rejection rates. Both absolute and relative frequencies of rejection do not differ significantly between male and female siblings (table 4.23). Similarly infants do not get on to female siblings significantly more often than males (table 4.24). However, female siblings pick up infants significantly more often than do male siblings at 2 weeks ($p < 0.002$) and this would account for the difference in time on between them (table 4.24).

The difference in time playing with male versus female siblings

Figure 4.39

Mean percentage of time infants spend with male and female older siblings. Vertical bars denote standard errors. ● male siblings (n = 10). ○ female siblings (n = 6).

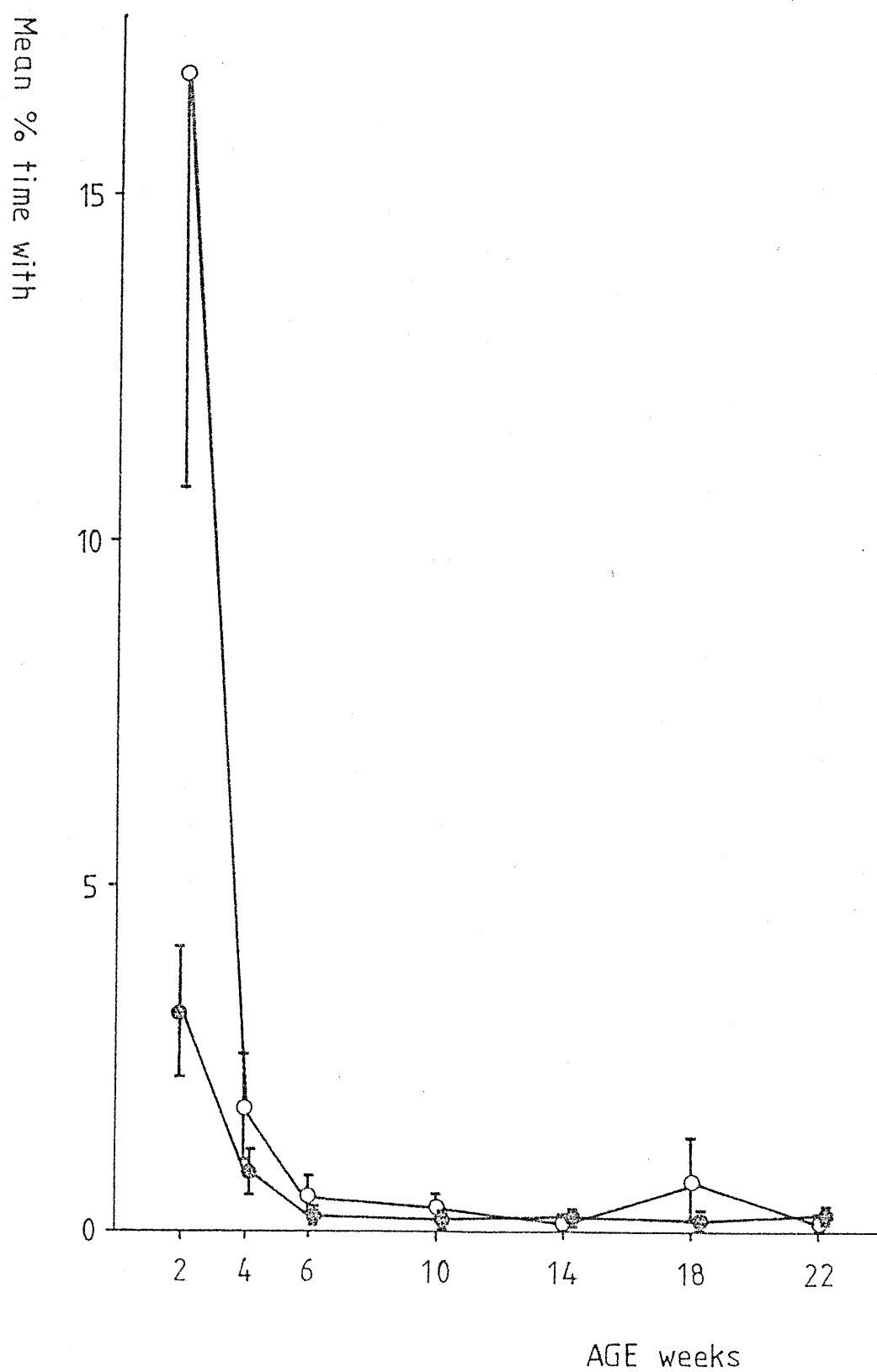


Figure 4.40

Mean percentage of time infants spend on male and female older siblings. Vertical bars denote standard errors. ● male siblings (n = 10). ○ female siblings (n = 6).

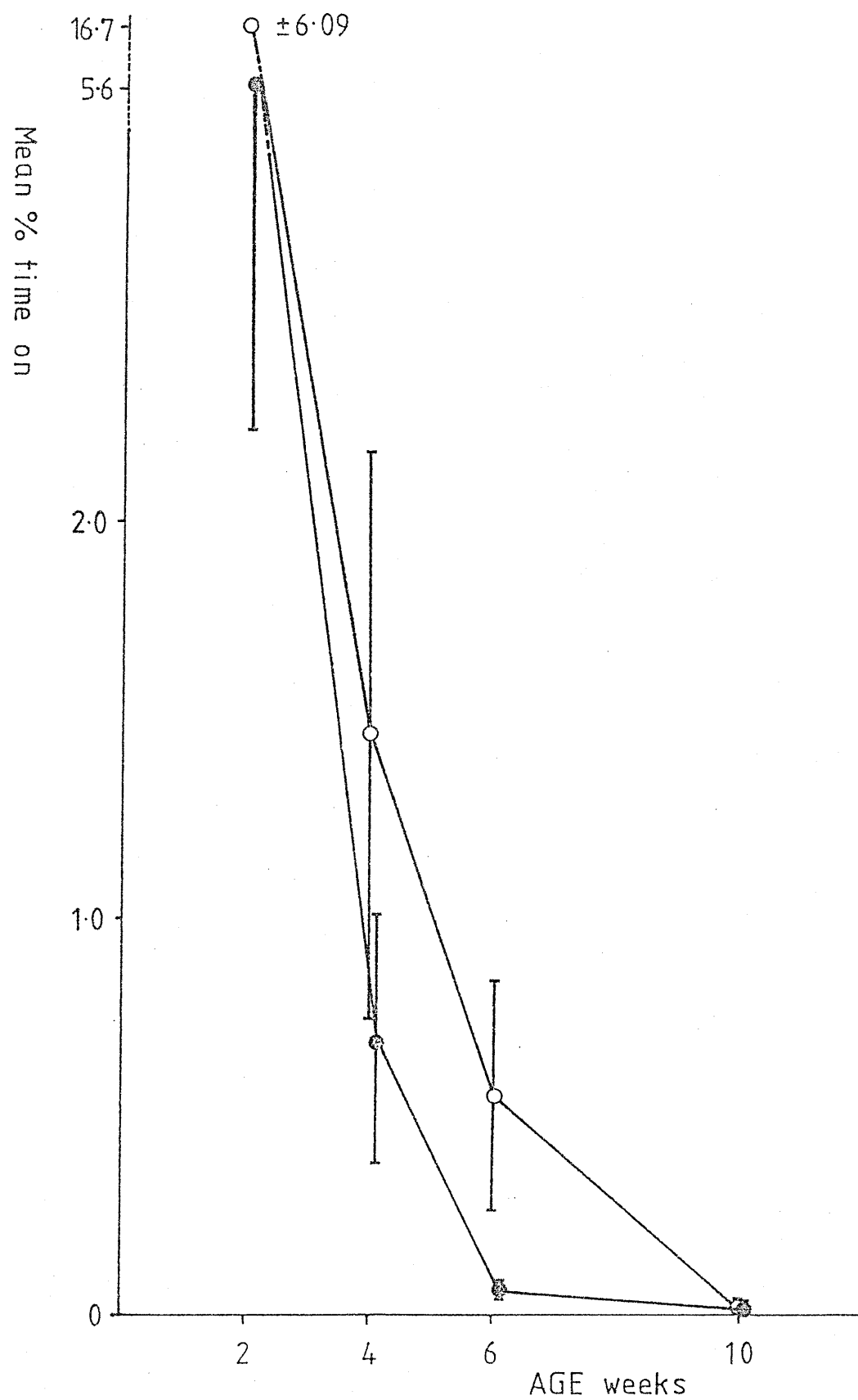


Figure 4.41

Mean percentage of time infants spend in contact with male and female older siblings. Vertical bars denote standard errors. ● male siblings (n = 10). ○ female siblings (n = 6).

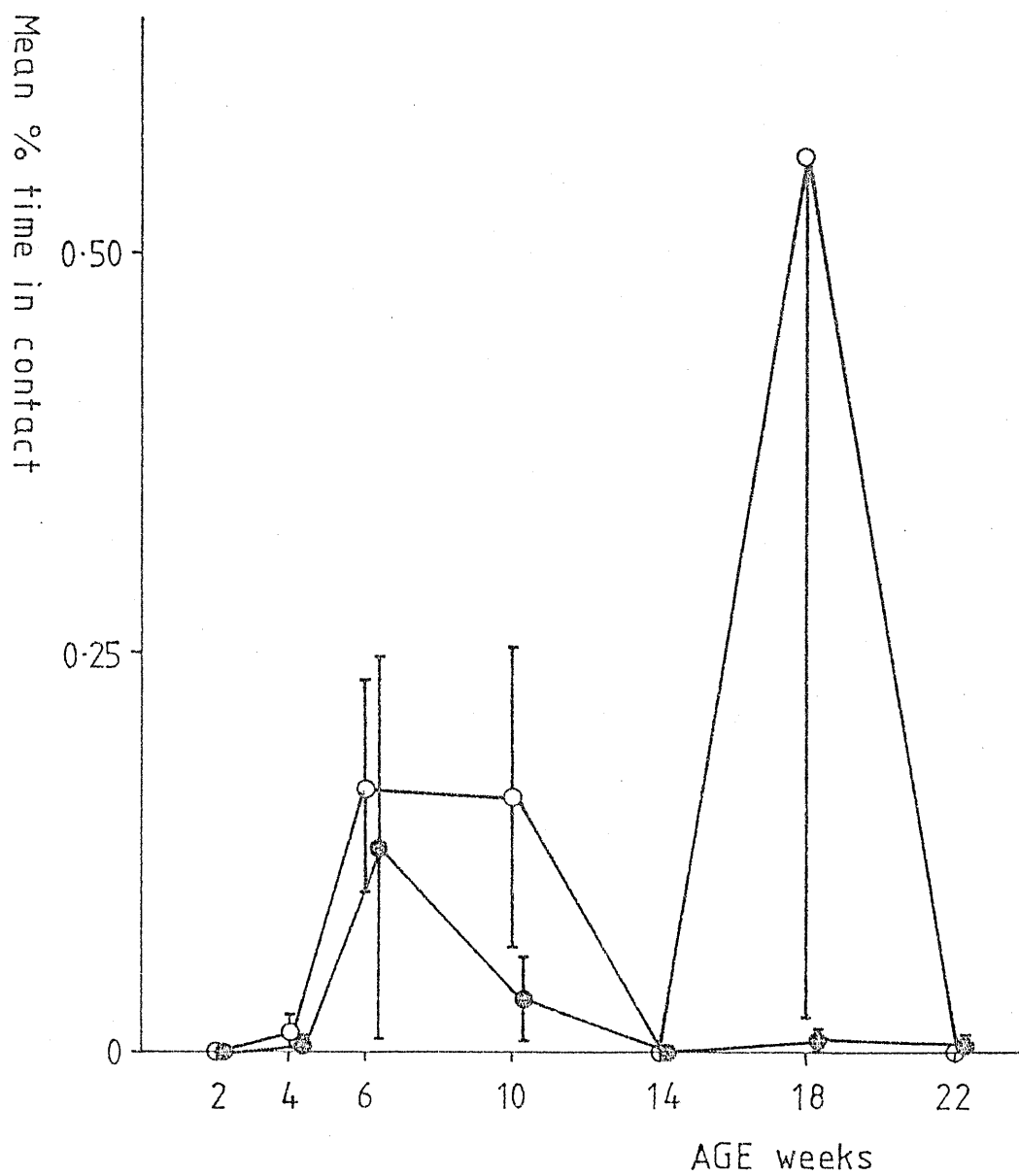


Figure 4.42

Mean percentage of time infants spend grooming with male and female older siblings. Vertical bars denote standard errors. ● male siblings (n = 10). ○ female siblings (n = 6).

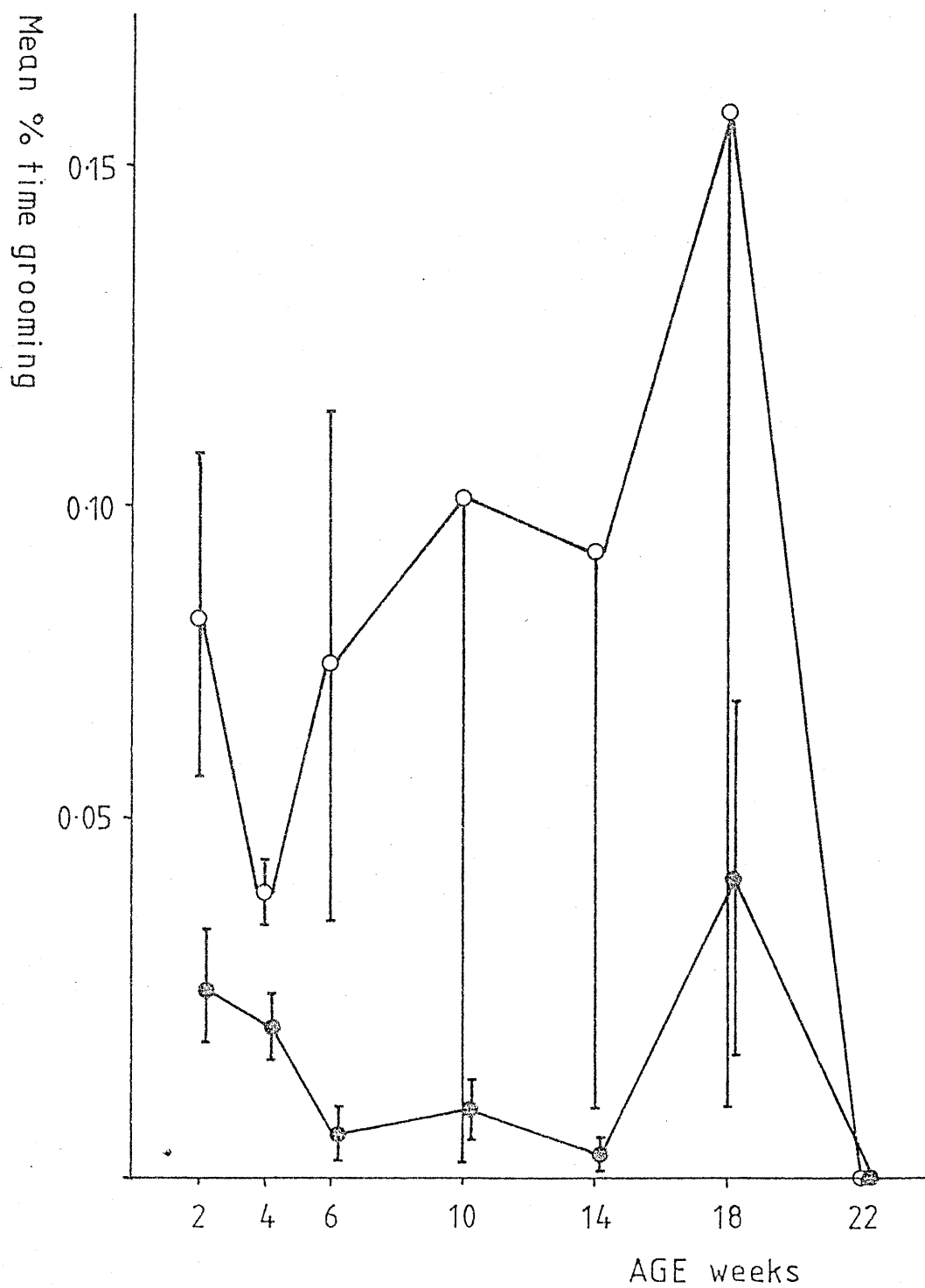


Figure 4.43

Mean percentage of time infants spend playing with male and female older siblings. Vertical bars denote standard errors. ● male siblings (n = 10).
○ female siblings (n = 6).

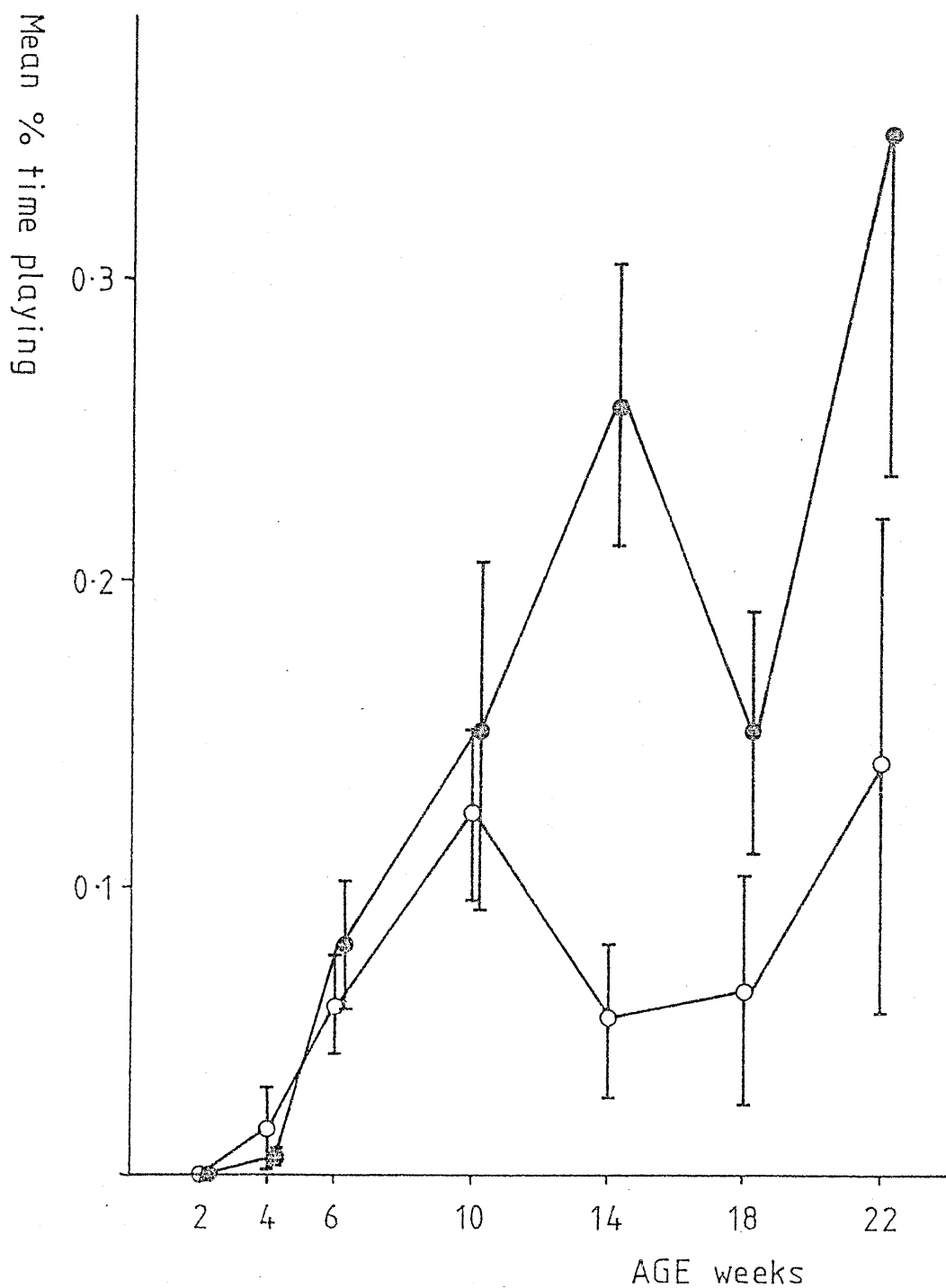


Table 4.23

Rejections by male versus female older siblings. Means and standard errors for absolute and relative frequencies of rejections for six female and ten male older siblings of infants. Results of two-tailed Mann-Whitney U tests between male and female siblings at each age showed no significant differences ($p > 0.05$).

Absolute Frequency Of Rejections

AGE/weeks	FEMALE SIBLINGS	MALE SIBLINGS
2	0	0.10 \pm 0.10
4	1.33 \pm 0.55	0.81 \pm 0.46
6	1.80 \pm 0.58	1.80 \pm 0.48
10	0	0.11 \pm 0.11
14	0.40 \pm 0.40	0.10 \pm 0.10
18	0.16 \pm 0.16	0
22	0	0

Relative Frequency Of Rejections

AGE/weeks	FEMALE SIBLINGS	MALE SIBLINGS
2	0	0.01 \pm 0.01
4	0.24 \pm 0.15	0.18 \pm 0.07
6	0.45 \pm 0.16	0.60 \pm 0.09
10	0	0.50 \pm 0.50

Table 4.24

Initiation of bouts of time on male and female older siblings. Means and standard errors for frequencies of infants getting on, and infants being picked up by, male and female older siblings. Probabilities (for results of two-tailed Mann-Whitney U tests between male and female siblings at each age) are greater than 0.05 unless otherwise indicated.

Infant Gets On

AGE/weeks	FEMALE SIBLINGS	MALE SIBLINGS	PROBABILITY
2	1.80 \pm 0.80	1.66 \pm 0.76	
4	4.33 \pm 1.05	2.00 \pm 0.53	
6	3.20 \pm 1.53	1.33 \pm 0.37	
10	0.20 \pm 0.20	0.11 \pm 0.11	

Infant Is Picked Up

AGE/weeks	FEMALE SIBLINGS	MALE SIBLINGS	PROBABILITY
2	8.40 \pm 0.51	2.55 \pm 0.64	< 0.002
4	1.66 \pm 0.66	0.70 \pm 0.26	
6	0.80 \pm 0.49	0	
10	0	0	

at 14 weeks is not due to infants or male siblings approaching each other more often (table 4.25). On the contrary, the only significant differences are at 4 and 6 weeks where infants approach female siblings more than males. There are also no significant differences between the frequencies of ignores by male and female siblings at any age. Other workers have found for various species that immature males play more frequently and more vigorously than immature females, for example captive and free-ranging rhesus monkeys (Hinde & Spencer-Booth, 1967a; Lindburg, 1971; Redican & Mitchell, 1974; Symons, 1978), various species of Macaca (Caine & Mitchell, 1979), squirrel monkeys (Baldwin & Baldwin, 1974), and possibly gorillas (Hoff et al, 1981b), though this has not been reported for marmosets. Volland (1977) reports that in common marmosets there were no play elements specific to one sex but that it was possible that they occurred with different frequencies depending on sex. Thus it may be that the greater amount of play with male siblings at 14 weeks is simply a reflection of a general tendency for male immatures to be more 'playful' than females. This cannot be verified from the present study since data on total frequencies or durations of play by older siblings were not collected.

These results suggest that in the case of common marmosets there is little difference in the way older brothers treat infants compared to the way older sisters behave. This is in contrast to studies of old world monkeys where female siblings exert a greater influence on infants than male siblings through spending more time with them and showing more behaviour towards them (for example see Bolwig, 1980, for baboons and pigtail macaques; Cheney, 1978, for yellow baboons; Lancaster, 1972, for vervet monkeys; Spencer-Booth, 1968, for rhesus monkeys). In this study, only at 2 weeks do female siblings pick up infants significantly more often than do male siblings, resulting in more

Table 4.25

Approaches to and by male and female siblings. Means and standard errors for frequencies of infants approaching male and female older siblings, and for male and female older siblings approaching infants. Probabilities (for results of two-tailed Mann-Whitney U tests between male and female siblings at each age) are greater than 0.05 unless otherwise indicated.

Infant Approaches Siblings

AGE/weeks	FEMALE SIBLINGS	MALE SIBLINGS	PROBABILITY
2	1.20 \pm 0.37	0.55 \pm 0.29	
4	7.16 \pm 0.83	2.90 \pm 0.48	< 0.002
6	14.80 \pm 3.12	6.44 \pm 0.76	< 0.05
10	20.20 \pm 8.29	9.88 \pm 2.00	
14	10.60 \pm 3.57	11.60 \pm 1.34	
18	10.33 \pm 4.19	8.70 \pm 1.19	
22	12.75 \pm 4.04	7.87 \pm 1.04	

Siblings Approach Infant

AGE/weeks	FEMALE SIBLINGS	MALE SIBLINGS	PROBABILITY
2	12.20 \pm 1.98	9.66 \pm 1.00	
4	15.00 \pm 3.08	10.70 \pm 0.88	
6	14.60 \pm 2.87	10.88 \pm 2.74	
10	11.60 \pm 5.44	10.77 \pm 2.50	
14	8.20 \pm 1.80	9.55 \pm 0.88	
18	12.00 \pm 2.80	10.00 \pm 1.33	
22	6.00 \pm 2.34	8.12 \pm 1.14	

time being spent on female than male siblings by infants at this age.

However, in the case of marmosets this distinction between male and female siblings would not be expected since, as adults, fathers are as important in caring for infants as mothers. Zucker and Kaplan's (1981) statement that alloparenting, i.e. caregiving by non-parents, is "a typically female behaviour" does not therefore hold for this species.

4.8) FAMILY DIFFERENCES

All nine infants used in Part I of the study came from three families. This is a very small sample size for families and if these families are sufficiently different from one another in their behaviour towards infants this could invalidate combining the data from their respective infants in means as has been done in presenting the results. The suggestion of different 'family backgrounds' for the infants became apparent during watches of the first three subjects. Each family seemed to behave differently towards its infants. Family A subjectively appeared tolerant and sensitive, family B appeared less tolerant and more controlling, and family C intolerant and sometimes indifferent (see tables 2.1 and 2.2 for family composition).

a) Social competence scores

To investigate whether or not these apparent differences were real, that is whether they influenced infants' development and whether they were consistent, a social competence score was devised. This was intended to be a composite measure of an infant's ability to cope with social situations and was taken at 22 weeks of age. This initial measure was decided upon because the differences subjectively apparent between

the families were social ones (i.e. differences in how caregivers behave towards infants) and if real could therefore be expected to influence the socialization of the infants. Thus infants from different families could be expected to behave differently in the face of situations requiring social skill. A composite measure consisting of several social 'skills' was therefore chosen as an initial attempt to differentiate infants from different families. If this 'crowbar' technique indicated family differences then other measures of social interaction could also be expected to show family differences and could then be investigated. Originally the social competence score was to consist of the mean of the following five measures:

- 1) The percentage of interruptions by the infant which are successful.
- 2) The percentage of interruptions by caregivers which are unsuccessful.
- 3) The percentage of food-stealing attempts by the infant which are successful.
- 4) The percentage of attempts by the infant to pick up younger siblings which are successful.
- 5) The percentage of attempts by the infant to rub off younger siblings which are successful.

The data for each of these measures is shown in figures 4.28, 4.30 and 4.31.

However, only four out of the nine subjects interacted with younger siblings (from the next offspring set) at 22 weeks of age, so the social competence score was reduced to the mean of measures 1), 2) and 3) above. Social competence scores for the nine infant subjects are given in table 4.26.

A between-litter - within-litter variance ratio (Barrett & Bateson, 1978) showed there to be no significant difference in the scores from the three families, however the sample size is really too small for

Table 4.26

Social competence scores (means of three percentage measures) of infants at 22 weeks of age.

INFANT NO.	FAMILY A	FAMILY B	FAMILY C
1		33.380	
2			18.648
3	30.792		
4		35.910	
5			24.706
6	49.603		
7		38.889	
8			33.986
9	60.806		

statistical analysis. Instead, it is possible to make comparisons by looking at the directions of differences in the scores of infants from different families. Berman (1978b) has used a similar method for small sample sizes in looking at mother-infant interaction in rhesus monkeys. Table 4.27 shows for the three infants from each family, how their social competence scores differ from the scores of the infants from the other families. Plus signs indicate larger scores, minus signs indicate smaller scores.

Infants from family A tend to have higher scores than infants from families B and C, infants from family B tend to have higher scores than family C infants and lower scores than family A infants, and infants

Table 4.27

Direction of differences in social competence scores between each infant from each family and the infants from the other two families. Each plus sign denotes that the infant in the lefthand column has a higher score than an infant in one of the other families. Each minus sign denotes the infant has a smaller score than an infant from another family.

SUBJECT NO.	OTHER FAMILIES						NO. PLUSES
	A		B		C		
Family A							
3			-	-	-	+ + -	
6			+	+	+	+ + +	
9			+	+	+	+ + +	14
Family B							
1	+	-	-			+ + -	
4	+	-	-			+ + +	
7	+	-	-			+ + +	11
Family C							
2	-	-	-	-	-	-	
5	-	-	-	-	-	-	
8	+	-	-	+	-	-	2

from family C tend to have lower scores than family A and family B infants. This indicates a possible influence of family background on the social skillfulness of infants at 22 weeks old. The most skillful infants come from the family whose members are most responsive towards their infants, and the least skillful infants come from the most indifferent family.

The tendency of absolute and relative rejection frequencies by fathers, mothers and siblings to be positively correlated, and similarly for the number of times infants climb on to different caregivers to be positively correlated, are further indications of the possibility of a 'family effect' (table 4.14).

Other behaviours which could be expected to be distributed differentially among families if the sensitive-controlling-indifferent continuum holds are tantrums, restrictions, ignores, aggression and time spent on caregivers.

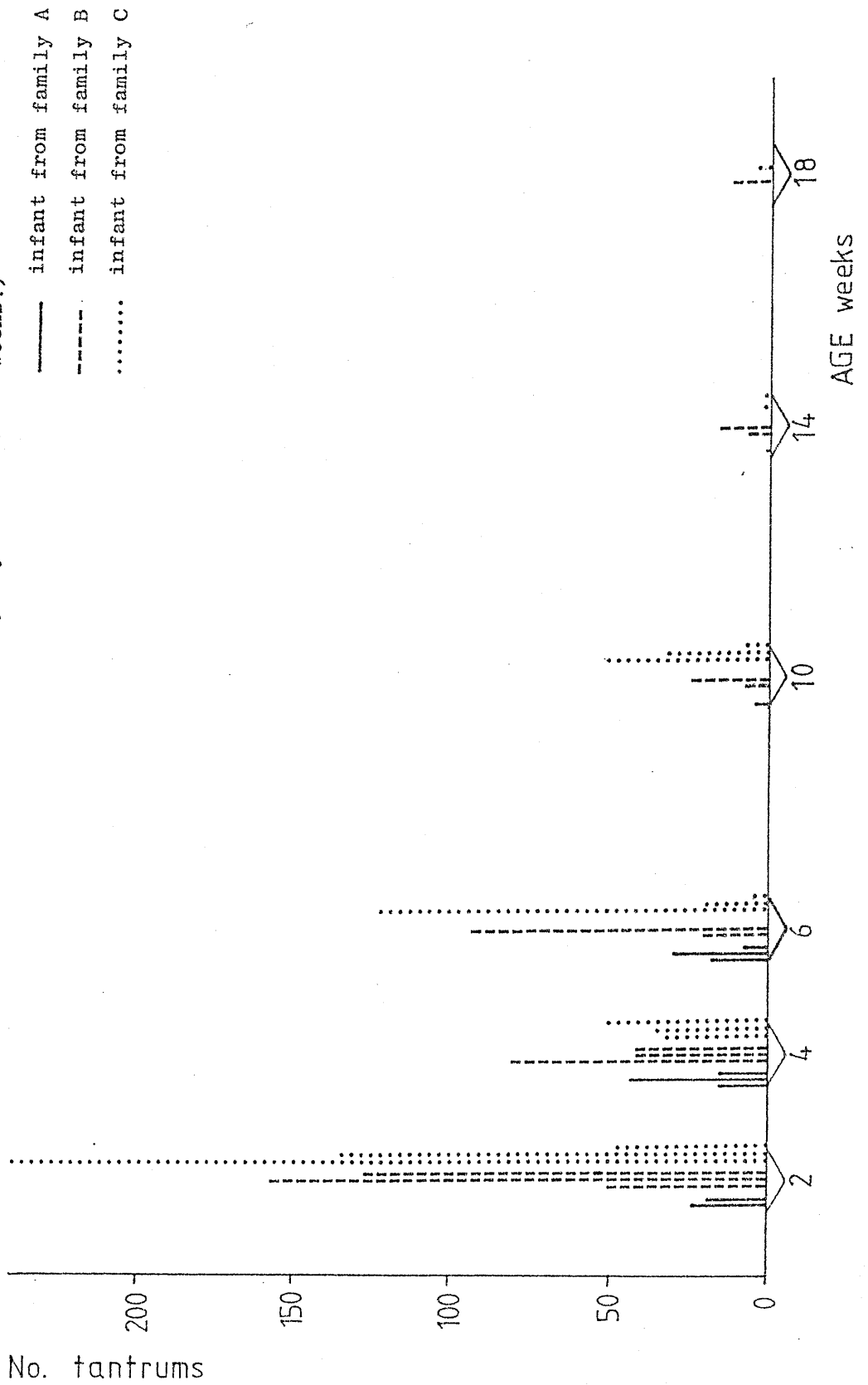
b) Tantrums

It could be expected that most tantrums would be given by the most distressed infants, and that infants in family C would be more distressed than those in family B, and those in family B more than those in family A. Hence it is predicted that if the apparent family differences are important, tantrums will be distributed $A < B < C$.

Figure 4.44 shows the total number of tantrums given by each infant from each family. It can be seen that the predicted distribution is not clearly borne out at all ages, but at some ages (e.g. 2, 6 and 10 weeks) differences are in the expected direction.

Figure 4.44

Total frequency of tantrums given by each infant at each age.
(No tantrums by any infant at 22 weeks.)



c) Restrictions

Restrictions by caregivers of infants' attempts to get off occur very rarely (figure 4.22), and the behaviour was seen only seven times during the course of all observations for Part I. However, in the context of family differences it is interesting to note that of these seven, five were performed by family B, two by family A, and none by family C. This is in line with the subjective assesment of the families made at the beginning of this section.

d) Ignores

If family C is the most indifferent it would be expected that this family would ignore infants more often than the other two families. Similarly, if family A is the most sensitive it should ignore infants least. Figure 4.45 shows that though the frequency of ignores of infants in families B and C are similar, in general infants from family A do tend to be ignored less than infants from the other two families, though the size of the difference depends on the age of the infants.

e) Aggression

Aggression in families towards infants would also be predicted to follow the trend $A < B < C$. Figure 4.46 shows the total aggression shown towards each infant in each family. Aggression in family A occurs less often than in families B and C from 2 to 18 weeks. The highest amount of aggression is shown by either family B or family C, depending on the age of the infants.

f) Total time on caregivers

Figure 4.47 shows the total time spent on caregivers for infants from each family. There is little difference between families except at

Figure 4.45

Total frequency of ignores given by caregivers to each infant at each age.

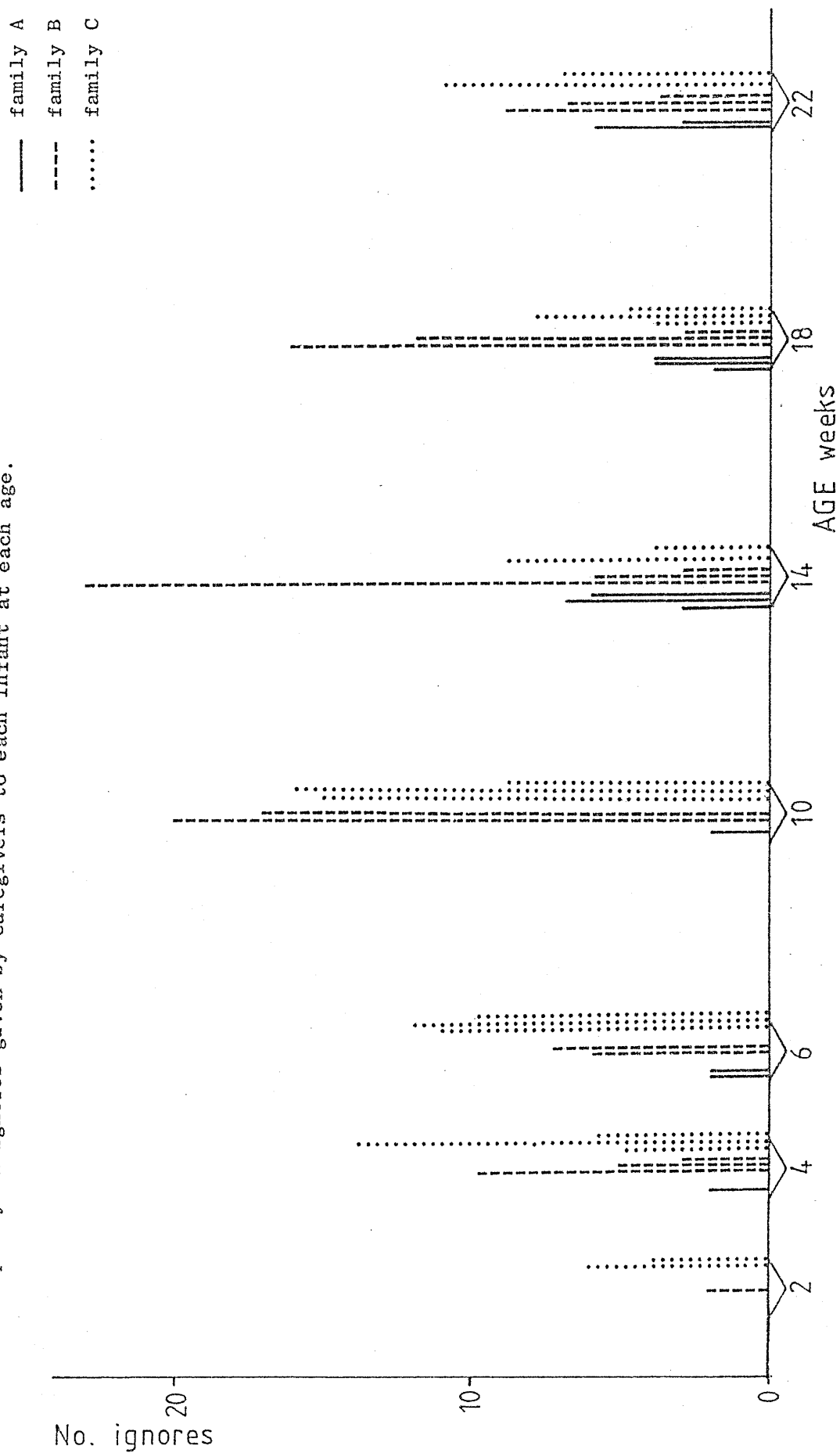


Figure 4.46

Total frequency of aggressive acts by caregivers to each infant at each age.

— family A
 ---- family B
 family C

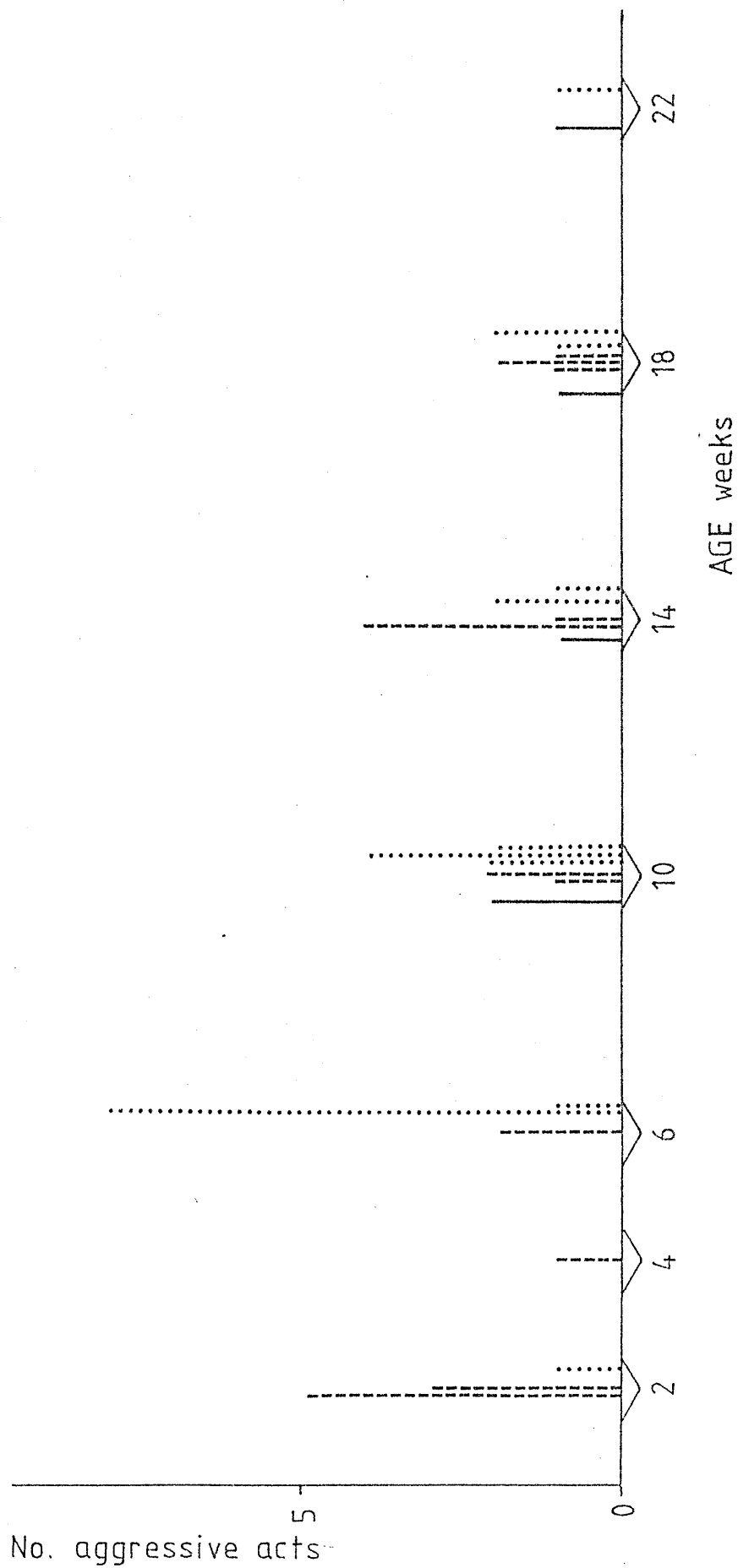
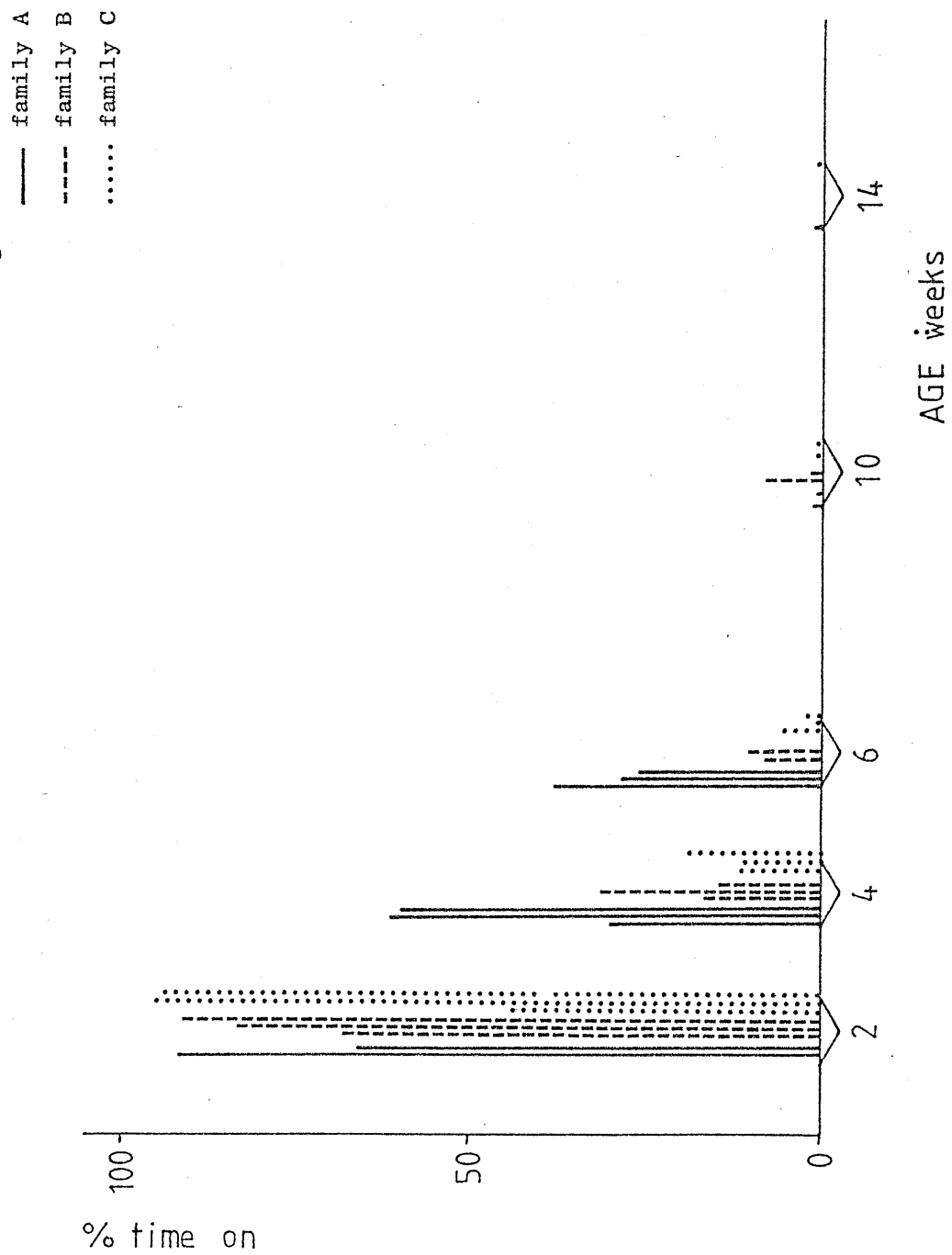


Figure 4.47

Total time each infant spends being carried by caregivers at each age.



4 and 6 weeks where there is a trend for more time to be spent on by infants from family A and less time to be spent on by infants from family C.

Differences in behaviour with respect to families are therefore small though in several cases results differ in the expected directions based on predictions from a subjective assesment of family differences. Although the data are inadequate for firm conclusions they indicate the need to consider the importance of factors concerned with family background, e.g. the identity of the parents, even when the focus of the research is on behaviour which can be generalised across infants. Nevertheless, given the small size of the differences, it seems not unreasonable to pool the data from the three families.

4.9) DISCUSSION AND HYPOTHESIS

From the foregoing sections it is clear that the quality of the infant's relationships with each kind of caregiver changes with age and that different kinds of caregivers come to have different relationships with the infant. The results are in general agreement with those of Ingram (1975a, 1977) though some details differ.

Ingram reported a drop in carrying by caregivers to minimum levels by 6 to 8 weeks, which is similar to the results given here. The decline is faster for fathers and siblings than for mothers in this study, but such differences are not apparent in Ingram's study. Mean bout lengths of time on diminish with age in both studies, and in both the relative frequency of rejections by caregivers rises rapidly over the first 6 to 10 weeks of infant life. The mother's relative rejection rate is lower than the father's at some ages in this study, whereas the reverse tends to be the case in Ingram's animals.

Ingram concluded that the infant's increasing independence from

its parents was, in the case of the mother, brought about by the mother, but in the case of the father the increase in independence was in some instances promoted mainly by the father, in others by the infant and in others by both. In this study, independence from fathers, mothers and older siblings is promoted primarily by the respective caregivers in each case.

Both studies report a greater involvement of female than male siblings in carrying and staying close to infants. In Ingram's study the difference in caregiving between male and female siblings is large for adolescent siblings but decreases by the time they are subadult. In the present study the siblings were adolescent, however the difference between males and females in carrying and time with infants was only significant when the infants were 2 weeks old.

Both studies show that time spent off by infants increases rapidly over the first few weeks (2 - 6) and then the rate of increase slows down. The combined %AP.I - %LV.I graph for this study showing the infant's role in maintenance of proximity to all caregivers is similar in form to Ingram's separate graphs for parents and siblings. Both show a crossing-over from caregiver to infant playing the primary role in proximity maintenance when the infants are 3 weeks old.

In this study, time spent carrying infants by different members of a family was not significantly inversely correlated, showing that caregivers do not make up for deficiencies in carrying by other caregivers in their family. Ingram however found that one parent often compensated for a lower amount of carrying by the other. Competition for access to infants was not seen in either study. She also notes that though different families show different individual patterns for rearing their infants, the overall patterns of feeding, carrying and time off were similar for all families. This was found in the present study.

For social play behaviour, both studies report similar findings in that infants play with their twins most often, their siblings next and their parents least. However no play with parents was observed in this study while it was observed by Ingram.

Some of the differences between these two studies may be due to different methods of observation and recording, or differences in husbandry. For example some of Ingram's families were kept freely in small rooms rather than being confined to cages, and families were housed with a variable number of offspring.

Box's studies (1975a, 1975b & 1977) on captive common marmosets also provide data which can be compared with this study. She notes that for carrying behaviour all members of a group participate but that there is great variability between family groups, and in the early weeks of infant life, infants may be carried most by fathers, most by mothers, or equally often by both. In this study fathers nearly always carry for longer than mothers at 2 and 4 weeks. Kingston (1969) states that after birth infants are carried by the male for the next 4 or 5 weeks. Similarities between Box's work and this study include the particularly sharp decline in time fathers spend carrying infants as infants get older, the fact that parents carry far more than siblings, and the sharp increase in time infants spend off after 2 weeks. She also notes that female juveniles (older siblings) are more involved with infants than male juveniles.

Box had larger family groups (six older siblings plus parents) and noted that infants were most often carried separately. In this study, with families of two older siblings plus parents, infants were most often carried together i.e. on the same caregiver, at least for the first four weeks.

Play began in Box's infants at 30 days of age, this coincides

with observations of play by 4 week old infants in this study, and as in this study, it occurs mainly with the twin. Stevenson (1978a) also indicates that play in common marmosets begins at 4 weeks of age.

Other Callitrichid species have also been shown to behave in a similar manner towards their infants. Vogt et al (1978) studied Saguinus fuscicollis and found that fathers carry more than mothers for most of the first 12 weeks of infant life, that parents usually carry more than siblings and that male siblings carry as much as female siblings. For the first few weeks twin infants are typically carried by the same individual, but as they grow older they are more likely to be found on different caregivers. Eppler (1975) reports similar findings for this species. Other species in which the adult male does much of the care-taking of the infant though all members of the group carry for some of the time include Saguinus oedipus (Hampton et al, 1966; Welker et al, 1981), Cebuella pygmaea (Christen, 1968) and Leontopithecus rosalia (Snyder, 1974).

All of this work on marmosets and tamarins has been carried out on captive animals. Virtually nothing is known of marmoset social development in the wild, the few field studies carried out so far have concentrated on ecology and group structure (for example Dawson, 1976; Neyman, 1980).

The social development of common marmoset infants seems to occur not as a series of stages but as a single continuous process involving detachment from parents and a shift in emphasis of attachments with siblings and twins. The closest form of contact between an infant and a caregiver (being carried) is replaced by sitting with individual caregivers and family huddling. This process of intimate contact decreasing rapidly in early infancy with a concurrent increase in other

forms of contact has also been noted in rhesus monkeys, chimpanzees, lowland and mountain gorillas (Hoff et al, 1981a) and lion-tailed macaques (Kumar & Kurup, 1981).

However the process in marmosets is different from that in, for example, macaques where an infant effectively leaves its mother to join its peers (Jensen & Bobbitt, 1967) since the infant has already developed relationships with its older siblings (through carrying) and its twin (close contact, and later play). Here, interactions with parents decline and interactions with siblings and twin become more active and vigorous as play becomes much more frequent. Infants also become more independent and spend much more time alone, exploring and manipulating the cage. The development of play may contribute to the decrease in parent-infant attachment (carrying) and promotion of infant independence (Harlow, 1969; Hoff et al, 1981b), or it may be a consequence of these processes.

Cause and effect in the development of behaviours are difficult to separate out in observational studies and may not in fact be the important issue. Relationships are reciprocal and continuous and it is difficult to conceive of either partner "causing" the behaviour of the other. For example, an infant may play more and thereby spend less time on caregivers, or by spending less time on caregivers, have more time to spend in play. The effect of one individual's behaviour on another will be a function of both animals' present and past behaviours towards each other, and that of any other animals present. The identification of causal relationships in the context of a continuous series of behaviours (i.e. interactions which form part of a relationship between two individuals) is less important than searching for underlying factors which can be used to explain and predict the variations in the behaviours observed.

Infants have different relationships with different individuals, and different infants may have different relationships with those same individuals. In the context of the care of infant marmosets, what behavioural parameters could explain this?

A simple model or hypothesis to explain the distribution of an infant's time and activities among the members of its family can be constructed on the basis of two related parameters, the tendency of an infant at a given age to seek a certain level of care, and the tendencies of family members to offer a certain level of care. A caregiving/care-seeking hypothesis is more complex in species with several caregivers, as in marmosets, than in species with only one main caregiver, as the infant is involved in several well-defined relationships simultaneously and as relationships between caregivers may affect their individual tendencies to offer care.

The hypothesis can be expressed most clearly if 'caregiving' is represented by a single, easily-measured activity. It has been shown in earlier sections that in the early weeks of life, most of an infant's time is spent being carried by caregivers. This is an obvious example of care and the amount of time on is an indicator of parental performance. For the purpose of describing and explaining the hypothesis, carrying will be equated with infant care for the first few weeks of life in the remainder of this chapter. Epplé (1975) has also used carrying as a measure of caregiving.

Clearly, however, care does not consist solely of individuals carrying infants about. The young animals must also be fed and kept clean. Other behaviours such as food-sharing and grooming could therefore also be viewed as care. When infants grow too large to be

easily carried, other means are required to provide the necessary security, comfort in fear-arousing situations and perhaps warmth. Under these circumstances contact, the sitting close to another individual, also becomes a likely candidate for the category care. This wider definition of care which includes several behaviours which benefit the infant at some cost (of time and the opportunity to engage in other activities) to the caregiver will be expanded upon in chapter 6.

Differences in the amount of care individuals are prepared to give, and in the amount infants seek, and the different ways these varying levels are combined in family groups, could account for observed differences in caregiving behaviour between different groups of animals. This explanation also allows for differences in group structure and group 'traditions' as these will include an element related to caregiving behaviour.

For example, if an infant perceives that the amount of care it

has received is less than the amount it seeks and if this is more than the amount caregivers will offer, it would be expected that infants would continue to seek care, that they would be rejected, and that caregivers would show no competition over which individual cared for the infant, and no compensation (see figure 4.48). This is the situation reported here. Time on declines over the first 6 weeks of life, infants increase the frequency with which they approach these caregivers, and the proportion of bouts of time on which they initiate, caregivers increase the frequency of their rejections, and time on different caregivers is not negatively correlated.

If however, the total amount of care that caregivers are prepared to give is greater than the amount the infant seeks, it would be expected that inverse correlations would be found between the amount of care different caregivers give to infants (see figure 4.49). This is the situation reported by Ingram, who found that carrying by parents was inversely correlated. This does not necessarily indicate compensation, since if an infant spends a large amount of time on one caregiver it may not require much time on all others.

However, if the amount of care offered by caregivers greatly exceeds the amount sought by the infant, it would be expected for caregivers to compete for access to infants, and that highly caring individuals would compensate for low amounts of care offered by less caring members of the group (see figure 4.50). Rejection of infants would still occur when individual caregivers had temporarily exhausted the amount of care they were prepared to give. Box (1977) noted what may be a kind of competition occurring in her common marmoset family groups when some individuals actively dissuaded some others from taking infants from them. However, this was usually parents preventing siblings taking

Figure 4.48

Caregiving/care-seeking model of infant social development.

I. More care sought than given. (See text for details.)

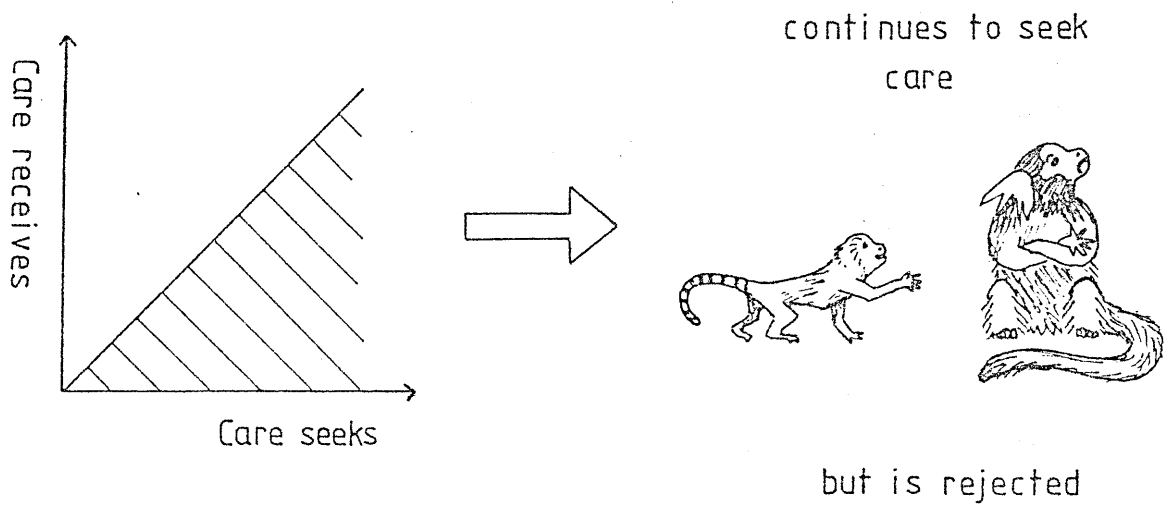


Figure 4.49

Caregiving/care-seeking model of infant social development.

II. More care given than sought. (See text for details.)

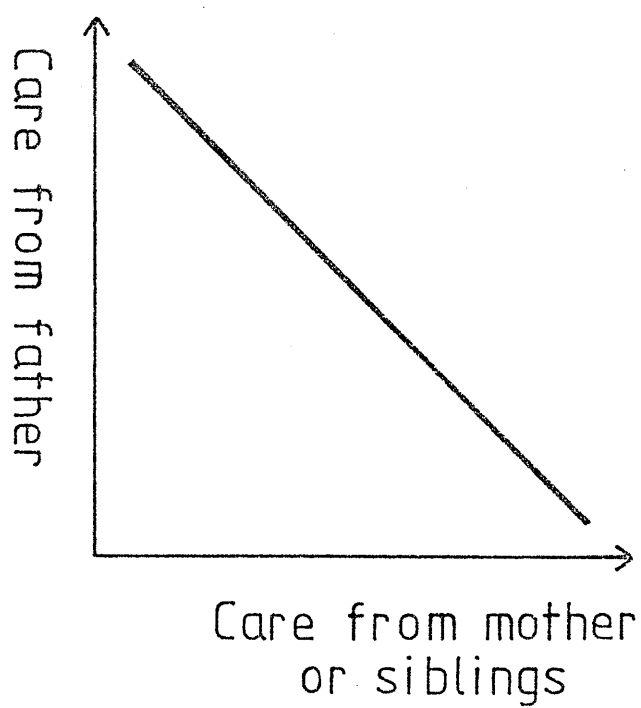
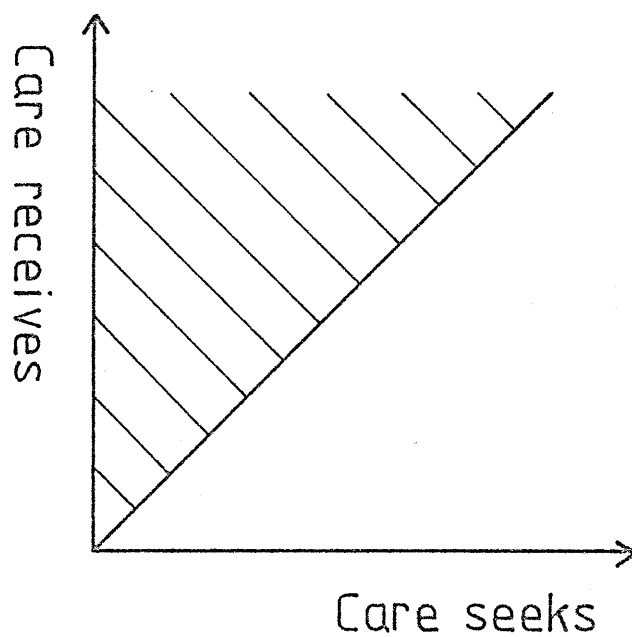
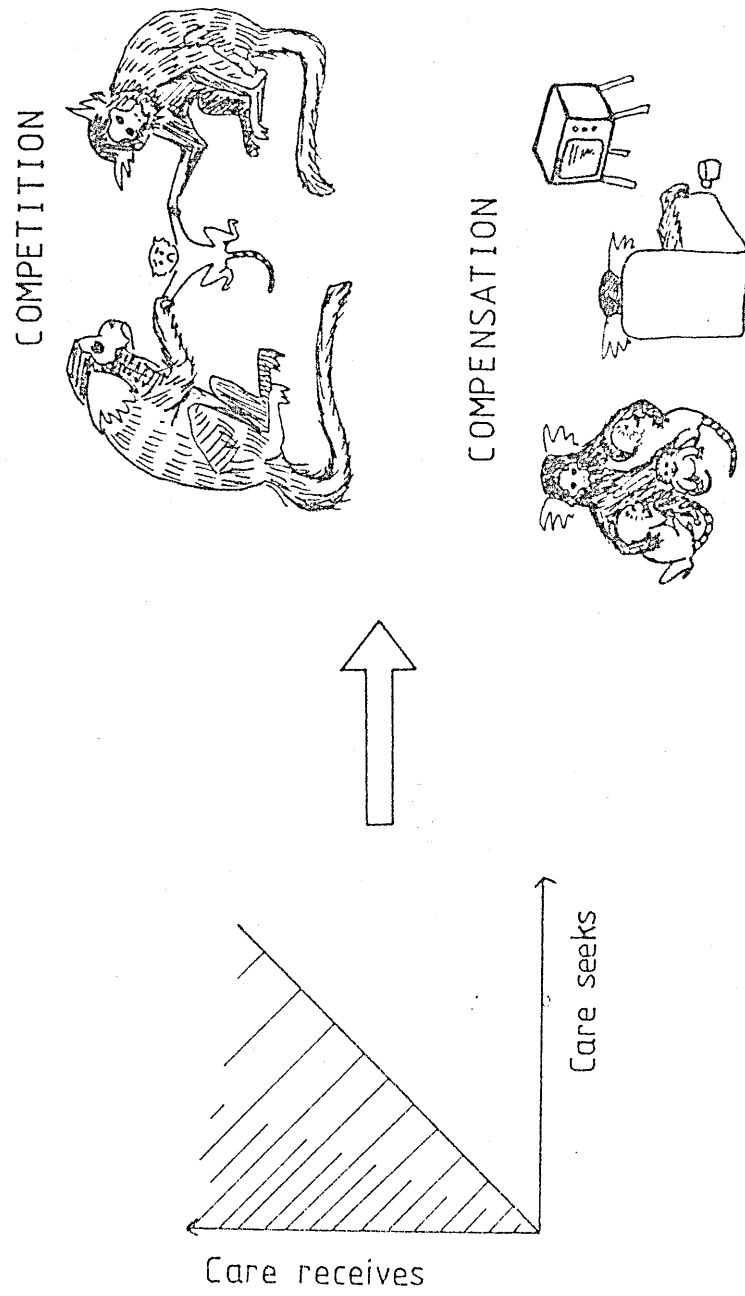


Figure 4.50

Caregiving/care-seeking model of infant social development.

III. Much more care given than sought. (See text for details.)



infants in the first week after birth, and may be more of a protective gesture against the vigorous and less experienced siblings who may inadvertantly damage very young infants. A similar observation by Eppele (1975) showed that when the infants of Saguinus fuscicollis are very young, some parents may chase away juveniles who try to touch the infants, and that this is more likely if the juveniles are unrelated.

The hypothesis leads to several interesting questions as a consequence of the multiple-caregiver situation in marmosets. For example, how does an infant work out the amount of care it perceives itself to have received? Is it indifferent as to the identity of the individual caring for it, or are different family members rated differently as caregivers? In other words, is the total care received by an infant the sum of that received from all caregivers, or is care weighted depending on which caregiver it came from?

Do caregivers have a fixed amount of care they are prepared to give to infants at each age/over all ages? If so, how does a caregiver work out the amount of care it perceives itself to have given? Is it indifferent as to which infant it is caring for, and to whether or not it is caring for (carrying) one or two infants simultaneously?

How does the combined amount of time all caregivers seek to give care, or are prepared to provide care if solicited, compare with the amount of time infants seek to be cared for?

The results presented so far indicate answers to some of these questions, and data from some other studies are suggestive. For example, in this study, there are significant differences in the relationships of infants with different caregivers at all ages (see sections 4.2) to 4.4)), 6 and 10 week old infants differ significantly in the number of attempts they make to climb on to different caregivers (see table 4.5),

infants groom different caregivers for different amounts of time (figure 4.5), they sometimes avoid being carried by caregivers and differ significantly in the degree to which they avoid different caregivers (figure 4.20), and there are significant differences in which caregivers are interacted with next following rejections and rub-offs (section 4.6)). This all suggests that infants do not rate caregivers equally. The fact that only mothers provide milk would also contribute to an infant's evaluation of care from different caregivers.

Horwich and Manski (1975) showed that infant colobus monkeys (Colobus polykomos and C. guereza) discriminated between adult female caregivers, tending to return to their mothers as soon as their locomotor abilities had developed sufficiently for this to be possible, and often resisting other females' attempts to pick them up. This was not merely because the infants required milk since they were also seen to nurse from non-mothers. Langurs however, have a more flexible system whereby adult female caregivers may be totally interchangeable. When mothers of captive infant Indian langurs (Presbytis entellus) were removed for two weeks, the infants transferred their attachment to another adult female. Upon return of the mothers, some infants remained with their adopted caregivers and made no attempts to re-establish their relationship with their mothers (Dolhinow, 1978 & 1980).

Box (1977) found that common marmoset caregivers were indifferent as to which infant they carried but tended to carry one infant more often than two. She also notes that a singleton infant received more care than individual twins. Ingram (1977a) also found this. This lends weight to the idea that caregivers may have a fixed amount of care to offer, as a single infant could take advantage of more of it than could individual twins. In this study, infants who have been rubbed off by a caregiver do not attempt to interact again immediately with that caregiver but are

more likely to try another caregiver (section 4.6)), thus behaving in a way which suggests a limit to the amount of time individual caregivers are prepared to devote to them.

Manipulation of levels of care-offering and care-seeking should allow fuller answers to be given to these questions through predictions derived from the hypothesis.

One issue raised by the caregiving/care-seeking hypothesis in view of the importance of fathers and siblings as well as mothers in caring for infants, is how this fits in with kin selection theory (Hamilton, 1964a & 1964b; Maynard-Smith, 1964; Trivers, 1972 & 1974). In particular, is it reasonable to expect that in certain situations compensation and competition between caregivers to care for infants will occur?

First it is necessary to explain the existence of multiple-caregiving in marmosets. Leutenegger (1973, 1979 & 1980) has argued that evolutionary dwarfism in the Callitrichidae has favoured the development of twinning as an adaptation to reduce foetal size at full term and ensure successful delivery (see also Ford, 1980). Monogamy tends to be found in species where males and females are of similar body size (Clutton-Brock & Harvey, 1976) and in primates this is restricted to arboreal species which are relatively small, e.g. marmosets and tamarins; Callithrix, Cebuella, Saguinus and Leontopithecus (Leutenegger, 1980), Goeldi's monkey, Callimico goeldii (Moynihan, 1976), owl monkeys, Aotus trivirgatus (Dixson & Fleming, 1981), titis, Callicebus (Moynihan, 1976), and the lesser apes, Hylobates and Symphalangus (Chivers, 1972 & 1974; Roonwal & Mohnot, 1977). Where ecological factors favour dispersal into small groups and morphological factors tend towards equivalent behaviour in both sexes, the female is left with a more or less permanent mate to assist in raising her offspring.

The effort put into raising offspring has been called parental

investment by Trivers (1972 & 1974), but Dawkins (1978) has suggested a more general term, altruism investment, since non-parents may also assist in the care of infants, as in marmosets. This investment is defined as any investment by the caregiver in an individual infant that increases the infant's chance of surviving (and hence reproductive success) at the cost of the caregiver's ability to invest in other infants. How an individual caregiver distributes its investment depends on the costs and benefits of the alternatives. In the case of marmosets, the female is producing twins and the cost of rearing two infants will be greater than that of rearing one. However if successful, the female benefits by having twice as many offspring. It is quite likely that a female on her own would be unable to rear successfully both offspring since even at birth twins may be the equivalent of a fifth of her body weight, and at 6 weeks one half. The cost to the mother if she alone had to carry the infants around would be very high. It is therefore to the benefit of the male to stay and assist the female in caring for the offspring. Since they are monogamous, the male can be sure that the infants are his offspring and by spending time caring for them he frees the female to forage unhindered and increases the probability that the young will reach maturity.

The cost to a male who did not care for infants would be very high since not only does he jeopardise the survival of that set of offspring, but he is unlikely to be able to go off and father others in the meantime as this would mean entering the territories of other males in which he may be attacked and have to fight. Maynard-Smith (1977) gives a mathematical model to show that monogamy with both parents caring for the young is an evolutionarily stable strategy in situations where two parents can raise twice as many offspring as one, or where the chance of a deserting parent re-mating is small.

Similarly, it is in the interest of siblings to help care for

infants before they (the siblings) are old enough to breed themselves since full siblings are as closely related to each other (50%) as they are to their own future offspring (50%), and in addition they will get valuable experience in handling infants. Epplé (1975) has suggested that marmoset males and females actually need to participate in the care of infants prior to becoming parents themselves in order to be able to provide adequate care for their own first-born infants. In addition, it has been suggested by Neyman (1980) that under natural conditions it may be very difficult for young adults (in this case Saguinus oedipus) to establish a territory. It is therefore in the best interests of the older siblings of a group to stay with their parents and help raise other siblings rather than to move away and possibly fail to raise infants of their own through being unable to establish a territory immediately. Extreme cases of this strategy in other species can lead to individuals having no young of their own but staying in their natal group and permanently assisting the breeding pair. This has been observed in African wild dogs (Lycaon pictus) where subordinate adult males (related to the dominant, breeding male) do not usually emigrate but remain with other male relatives and care for their pups (Frame et al, 1979). Black-backed jackals (Canis mesomelas) may also stay and assist their parents in raising the following year's litter and it has been shown that they can gain more (in terms of fitness) by doing this than by finding a mate and rearing a first litter of their own. Each older sibling caregiver adds about 1.7 pups to a litter raised by its family, whereas the reproductive success of a breeding adult without extra helpers is on average 1 pup per litter (Montgomerie, 1981).

Neyman was unable to verify whether or not the adult caregivers in her tamarin groups were related to the breeding pair (i.e. siblings or adult offspring), but did observe one pair of infants born into a

group which were still part of that group three years later when the study ended and had therefore been fully mature for over a year.

Marmoset social organisation is thus compatible with both kin and individual selection. This problem has also been addressed in bird species which have helpers at the nest and it has been found that in some instances individual selection is sufficient to account for the helping behaviour. Kin selection however, would appear to be significant in the most common cases of help, that is, offspring helping parents. Brown (1978) gives a useful review of this area.

On the questions of whether compensation and competition between caregivers to care for infants are compatible with kin selection theory, compensation can be seen as an insurance policy against short term deficiencies in another individual's caregiving abilities. It would be advantageous, up to a point, for an animal under certain conditions to be able to give more than its normal level of care. Such conditions might include the animal's mate being injured or debilitated, or an older sibling which was also a caregiver leaving the group or being removed by a predator. This would ensure the infants' immediate survival. This arrangement has been found to occur in the biparental cichlid (Aequidens paraguayensis). If either parent is removed experimentally there is an increase in the parental care of the remaining partner so that the amount of care equals that exhibited by both parents together in a normal pair (Mrowka, 1982).

However, animals which permanently gave more care would be penalised since other individuals would then be able to take advantage of this by giving less care. Since levels of caregiving have presumably evolved along with the species' other abilities, any permanent increase over the normal level will be maladaptive to that individual and is likely to make it less efficient at other activities.

This leads to the idea that individuals have a 'normal' level of care which they are prepared to give. To be most efficient the animals should be at or near this normal level most of the time, i.e. in normal situations of twin infants the animals are giving a level of care which is sufficient for both twins to survive. It is unnecessary and inefficient for them to give any more care than this, so this will have been gradually fixed by evolution as their 'normal maximum' level of care. This assumes that ecological conditions in their natural equatorial and tropical forest environment have not changed substantially over their evolution, since altered conditions may require altered behaviours to cope. Though nothing is known of the ancestors of living callitrichids, Hershkovitz (1977) suggests that their anatomy and behavioural adaptations were probably established early on and would have changed little in an equatorial habitat that probably remained relatively stable throughout most of the Cenozoic era.

If this is the case, and animals have a particular level of care which they are most likely to give, it is possible to envisage situations in which caregivers may compete over access to infants. For example, where there are fewer infants than normal (singletons instead of twins) and where there are more caregivers than normal (extended family groups). It has already been noted that single infants may receive more care than individual twins (Box, 1977; Ingram, 1977a). In the wild, it is presumed that on reaching sexual maturity young adults move out of their natal group to set up new groups and reproduce (Kleiman, 1979), so abnormally large numbers of caregivers are unlikely to be found. However, animals in captivity have been kept in much larger groups, for example 18 to 20 individuals including offspring 6 or 7 years beyond the normal age of sexual maturity (Kleiman, 1979). In these conditions the adult female appears to suppress ovulation in

her daughters through the action of pheromones (Hearn, 1977) and there is an excess of caregivers. In this situation it would be possible to test whether or not competition between caregivers for access to infants actually occurred, as would be predicted by the caregiving/care-seeking hypothesis. Varying the numbers of caregivers would also answer the question of how the combined amount of care offered by all caregivers compares with the amount of care sought by infants.

In one study where common marmosets were housed in large rooms containing family groups of up to twelve individuals infants were not observed to be off caregivers before about 5 weeks of age. This contrasts with the present study where infants are off for approximately 10% of the total time observed as early as 2 weeks of age (figure 4.10). This contrast is to be expected from the caregiving/care-seeking hypothesis since approximately twice as many caregivers are available to carry the infants (Bucher, 1980 & pers. comm.). Observations of these animals also suggested that competition was occurring. Mothers were seen to push away siblings who were attempting to groom infants and siblings were seen to interfere with each others' attempts to take infants from parents. Carriers actively prevented other individuals taking infants from them by leaving, aggressive stares, grasping, biting and "erh-erh" vocalizations (Bucher, 1980).

This line of investigation was not possible to follow up in this study since constraints on the amount of space available did not allow the use of larger cages which could take more animals. Instead, it was decided to test the hypothesis by making a series of predictions as to what would happen if caregiving levels were altered, and then to alter those levels and make observations to record whether or not behaviour did change in the predicted direction.

From birth, infants are communicating their state and their

needs to their caregivers. If their signals are accurately perceived and appropriately responded to, the resulting caregiver-infant relationship is characterized by synchrony and is such that it would be expected to facilitate infant development. But if a caregiver's responsiveness is altered by, for example, the administration of a behaviour-modifying drug, the relationship will be altered, and development changed. If the drug causes specific behaviour changes, changes in relationships should be predictable from a model of normal development. Infants may "do better" than predicted if other caregivers accept and allow for changes in the behaviour of the drugged animal, though compensation by parents and siblings was not seen to occur in the results of Part I.

It was therefore decided to use a drug to alter caregiving levels. An alternative method would have been to remove a caregiver from the group for a while, i.e. a separation study, but the effects of this would have been as pronounced on other members of the group as on the infant, and the disruption among other caregivers caused by an individual's disappearance and return would have masked any effect due to the reduction in the total amount of care available to the infant. This has been seen in rhesus monkeys where infants whose mothers were removed for 13 days received less adequate maternal care when their mothers were returned than did infants who had themselves been removed, because mothers removed and then re-introduced to the group were pre-occupied with re-establishing relationships with their group companions, and were therefore less attentive to their infants (Hinde, 1977).

The following predictions were made to be tested in Part II assuming the drug to be used would cause drugged animals to offer a reduced amount of care to infants:

- 1) If the infant receives less care, its attention will be diverted

from non - care-seeking, socializing activities such as play, to more direct care-seeking activities.

2) With the drugged animal offering less care, the infant will seek care from other caregivers, in order of preference. That is, it will seek care from those rated higher as caregivers (i.e. more preferred family members) more often than those rated lower.

3) If caregivers do not compensate, the amount of care offered by different individuals (excluding the drugged animal) is expected to be in the same relative proportions as in the undisturbed situation (except in the unlikely event that all animals compensate to exactly the same degree to make up for the deficiencies of the drugged animal).

4) In contrast to 3) above, if some caregivers do compensate for the reduced total amount of care, those caregivers will give proportionately and absolutely more care than in the undisturbed condition.

5) If caregivers have a maximum level of care and this is close to being reached in the normal situation, infants are expected to spend more time off and in family huddles when the total amount of care is reduced by drugging, than in the undisturbed situation.

6) If caregivers promote infant independence by rejections and generally reducing their care and attention to the infant (Hansen, 1966; Hinde & Spencer-Booth, 1967a & 1968; Jensen et al, 1969 & 1973), infants would be expected to become independent earlier if care is reduced by drugging.

These predictions were investigated by repeating the observation schedule used in Part I with the addition of drug administration on a further sample of infants to give precisely comparable results. This constituted Part II and the results are given in chapter 6. The selection and testing of the drug to be used are described in the following chapter (5).

A further question raised by administering drugs to alter

caregiving behaviour is how long do the effects last? The effects of altered caregiving on the infant may disappear when the immediate effects of the drug on the caregiver wear off, or they may persist for longer. Animals which experienced altered caregiving levels as infants may behave differently as caregivers themselves later on in life (see Harlow et al, 1966). This question will also be investigated partly in chapter 6 and further in chapter 7.

CHAPTER 5 - Preliminary Drug Testing

5.1) REQUIREMENTS

The aim of the preliminary drug tests was to find a substance suitable for use as a tool in modifying infant-caregiver relationships in such a way as to test the model of infant social development obtained from observing the undisturbed family groups in the first part of the study.

The first problem was which particular relationships to modify. It was felt that the subject's mothers should not experience drug administration since they would at the time be pregnant with their next set of offspring, and the possibility that chemically altering the mothers' behaviour might affect the infants 'in utero' could not be ruled out. Substances given to a pregnant mammal can pass to the foetus from the mother's bloodstream both across the placenta (by diffusion into the infant's circulatory system), and after parturition via the milk (by diffusion and reversed pinocytosis into the mammary gland alveolae). This is well known in humans and other mammals (Cole and Hailey, 1975; Julien, 1975; O'Brien, 1974; Vorherr, 1974). For example, the barbiturate secobarbital when administered to human mothers intravenously during labour, passes across the placenta in significant amounts and blood levels in the mother and in the newborn infant can be almost identical (at about four micrograms per millilitre) ten minutes after injection (Roote et al, 1961). Any drug given to the mother has this potential of entering the infant (O'Brien, 1974). Useful reviews of this area are given by Aleksandrowicz (1974) and Bowes et al (1970).

The developing brain and behaviour are most vulnerable to

modification by environmental factors (e.g. drugs) during the 'growth spurt' period of the brain. This sensitive time falls within the first third of pregnancy in humans (Dobbing and Smart, 1974; Goldstein et al, 1968). In the marmosets, the most appropriate time for modifying the mother's behaviour by drug administration would also fall within the first third of her next pregnancy. This has to be prevented since the next offspring set will contain another infant subject and it is desirable that all subjects experience conditions as similar as possible so that data from all can be meaningfully combined and compared.

Excluding the mothers leaves the fathers, older siblings and twins whose behaviour could be modified. The best time to interfere with relationships for maximum effect is at the time when the individual involved is at its most important to the infant, that is, when that particular infant-caregiver relationship is clearly defined and well developed. Such stages can be seen in the cases of the father and of the older siblings, where interactions with the infant vary considerably in quality and extent depending on the age of the infant (see chapter 4). However, in the case of the infant's twin the relationship appears relatively more uniform throughout the period studied.

It was decided therefore not to interfere with the mothers' or twins' behaviour, but to alter the infants' relationships with their fathers and with their older siblings, at ages appropriate to their importance as caregivers to their infants.

The second question to be answered was which was the best way to alter these relationships. Using drugs an animal could be made to be either more active and outgoing, by using stimulants such as amphetamine, cocaine or methylphenidate; or it could be made to be more passive and withdrawn, using sedatives such as barbiturates or benzodiazepines, or tranquillizers including phenothiazines or haloperidol. If an animal is

given a stimulant this will not be selective but will make the animal more active in relation to all other individuals around it , and not just the infant subject. This would be likely to alter radically all the relationships in the group, via the links in the social nexus, (see chapter 1; Hinde, 1975, and 1976; Nadel, 1957) between the drugged animal, the other individuals and the subject, and thereby vastly complicate the issue of precisely which relationship change was affecting the infant's behaviour. This 'whole-group' effect is likely to be less important if the animal is simply made to be more passive, to interact less, to 'take the initiative' less. As a result of this, the effects on the infant's behaviour would be less difficult to interpret. There is also less risk of injury or damage due to drug-induced hyperactive or aggressive individuals.

It was therefore decided to alter the caregivers' behaviour such that social interactive behaviour was depressed. This would be expected to cause relationships to become less intense, and less controlled or dominated by the caregiver, who would become more passive and tolerant. By comparing the infants' behaviour in the second part of the study, where the drugs would be used, with the behaviour expected on the basis of the observations in the first part of the study, the undisturbed phase, the validity of the model of infant social development could be tested.

A preliminary study of the results from the undisturbed infants showed that fathers were of particular importance when the infants were four weeks of age, spending more time carrying, grooming and with infants than other caregivers. Older siblings had most impact at around 14 weeks, becoming important play partners (see chapter 4 for details). It was therefore decided to take these ages as appropriate times for the administration of the behaviour-modifying drug.

Following the same observation schedule as for the first part

of the study (see chapter 3), the drugged monkey's behaviour needed to be affected for about four days in order that all the watches could be completed at that age. As the procedure of catching and removing an animal for injection seems to cause a degree of excitement and disturbance among the other animals in the same room, including possibly other subjects from other families which may be being observed that week, it was necessary to keep this activity to a minimum, i.e. by using a drug whose effects would last the four days required, thereby necessitating only a single administration per animal per age.

In summary, a drug was required which could be injected to cause a reduction in social interactions over a period of four days.

5.2) BACKGROUND

A vast amount of research involving animals (including man) and behaviour-modifying drugs has been carried out, both with regard to testing new pharmaceutical products (for example fluphenazine, a derivative of which is later used in this study, see Craver et al, 1965; High et al, 1960; Laffan et al, 1960), and also in the search for cures for such problems as drug abuse and addiction, for example in the study of amphetamine-induced behaviours (Haber et al, 1981; Scraggs and Ridley, 1979).

Most of the pharmacological work is concerned with the study of the drugs themselves, their site of action, metabolic fate, biochemical and physiological effects, and side-effects. For example, Dreyfus et al (1971) report in detail the metabolic fate of radioactive carbon labelled fluphenazine in dogs and rhesus monkeys. They give the proportion of the dose administered excreted via the urine, faeces, bile and expired air, and the precise localization of the metabolites in the

dogs' tissues. Jenner et al (1979) studied the extrapyramidal reactions induced by various neuroleptics in baboons and rats, and Kjellberg and Randrup (1972a) the stereotypies produced by amphetamine in vervet monkeys (Cercopithecus aethiops). Bunney (1977) reviews work carried out on the mechanism of action of antipsychotic drugs and on predicting their therapeutic efficacy. Much of this research is based on the assumption that knowledge of where and how therapeutically effective drugs act in the central nervous system may provide significant clues as to the pathology underlying the various mental disorders these drugs are used to treat.

Clinical research concentrates on human social and medical problems associated with drugs and relies mainly on data from patients already undergoing treatment, or on experiments using volunteers (for example, Bunney et al, 1979; DiMascio et al, 1967; and see Squibb, 1978 for further references).

A third area in which drugs are being investigated is in attempts to produce and simulate neuroses and psychoses in animals in order that the etiology of the diseases may be studied in detail. Examples include paranoid schizophrenia (Gambill and Kornetsky, 1976; Haber et al, 1977; Haber et al, 1979; Ridley and Baker, in press), Parkinson's disease (Goldstein et al, 1979), extrapyramidal reactions (Diamond and Borison, 1979; Jenner et al, 1979), and also separation-induced depression (Kraemer and McKinney, 1979; Suomi et al, 1978).

In none of these areas are the precise behavioural effects of the drug, and in particular its effects on social behaviour, given full consideration. An exception, at least to a certain extent, occurs in the third area above where Ridley's group (Ridley et al, 1979; Scraggs et al, 1979) divide the common marmoset's behaviour into a small number of very broad behavioural categories and measure how the frequencies of

occurrence of these change with administration of amphetamine, haloperidol and apomorphine. The categories consist of 1) checking, i.e. movements of the head, 2) activities, i.e. movements of part of the body, including eating, drinking, autogrooming and object manipulation, 3) contact, any type including allogrooming, fighting, playing and sexual activity, 4) locomotion, and 5) inactivity. This approach to the study of drugs is a relatively novel one. See for example Scraggs and Ridley (1978) for (crude) behavioural effects of amphetamine in the common marmoset, Schlemmer et al (1980) for apomorphine in stump-tail macaques (Macaca arctoides), and Gambill and Kornetsky (1976) and Ellison et al (1978) for effects of amphetamine on social behaviour of rats housed in colonies.

Crowley et al (1974) looked at the effects of four different drugs, ethanol, methamphetamine, pentobarbital and morphine, and compared their relative effects on members of a captive pigtail macaque (Macaca nemestrina) troop. They showed that ethanol produced ataxia, regressive playful fighting typical of juveniles and an increase in the ratio of heterosexual to autosexual behaviours. Pentobarbital reduced submissive behaviours, increasing the dominance-to-submission ratio. (The dominance-to-submission ratio is the ratio of frequencies of 'dominance' and 'submission' behaviours, i.e. dom./dom.+subm. Nine types of dominance behaviours were recorded including open mouth threat, biting and pursuit, as were nine types of submission behaviours including grimace, lip-smack, withdrawal and flight.) Methamphetamine decreased the dominance-to-submission ratio and produced hyperactivity, stereotypies and "social unrelatedness", i.e. behaviour not in relation to current social stimuli. Morphine blocked sexual behaviour without impairing motor activity.

Of particular relevance here is work done by Schiørring

(Schiørring, 1979; Schiørring and Hecht, 1979) on the changes in social behaviour of vervet monkeys given low acute doses of d-amphetamine. Amphetaminized animals (0.1 - 0.7 mg/kg) in small social groups typically became socially isolated and withdrawn, and social behaviour patterns were disrupted or eliminated. Rank order changes between females in relation to the amphetamine-treated male sometimes occurred. When amphetamine was given to adult female with infants parental care was disrupted as the mothers became isolated. They failed to respond to the calls of their infants and showed behaviour in which stereotyped self-grooming and "staring into space" were predominant. The infants responded to this either by increasing approach-avoidance movements or by sitting quietly close in front of the mother. Increased approaches by infants resulted in active rejection by the mothers. Mothers did not react with the typical ventral-ventral grasping to either the infants' sitting close, or to their calls, and appeared totally to lose interest in their infants.

The effects of drugs administered to cure illness on an animal's behaviour in a social situation are of vital importance since many drugs can have undesirable behavioural side-effects in addition to their desirable medical effects (for example amphetamines, see Kjellberg and Randrup, 1972^b). Similarly, the results of drug addiction are at first primarily behavioural and it is these indicators which need to be picked up early on to detect and allow assistance to be given to those who might otherwise become physiologically dependent. As Kraemer and McKinney (1979) have noted, previous studies have frequently used imprecise behavioural scoring systems which do not, for example, discriminate between sedation ("sleepiness") and depression (reduced activity). They report studies on the metabolic basis of the 'despair' response of rhesus monkeys to social separation which involve the use of

drugs to alter catecholamine metabolism, thought to be involved in this response, and conclude that previous results from nonhuman primate social studies (e.g. McKinney et al, 1971; Redmond et al, 1971) could be reflective of the sedative and not the depression-potentiating effects of the drugs. That is, there are problems of interpretation as a result of inaccurate behavioural studies on the effects of the drugs. It is this type of investigation of the purely behavioural effects of drug administration that was the aim of the preliminary drug tests described here.

Finally, there is the role of drugs as experimental manipulators of responses in the study of normal, as opposed to neurotic or psychotic, behaviour. Humphreys and Eimon (1981) have recently used chlorpromazine and amphetamine to alter play and other social behaviour in investigating the reinforcing value of play for rats. Drugs altering serotonin neurotransmission have been used to discover the relative contribution of serotonergic systems in the mediation of grooming, approaching, resting, locomoting, being solitary and being vigilant in vervet monkeys (Rayleigh et al, 1980). Drugs such as tranquillizers and sedatives are also used to "tame" animals which may behave aggressively in captivity, and as preanaesthetic medication in humans (Green, 1979; Heise and Boff, 1961). Usefulness as a tool was the ultimate requirement of the drugs to be tested here.

Pharmacological effects of drugs differ greatly from species to species, even if closely related (Aleksandrowicz, 1974) so it was considered vital to carry out preliminary tests on the marmosets if drugs were to be used experimentally, particularly in view of the relatively small number of studies which have used drugs to investigate the normal behaviour of animals (see above).

5.3) SOURCE AND SUPPLY

Two classes of drugs can be used to depress behaviour. The first includes sedatives such as barbiturates (e.g. phenobarbital and pentobarbital), antianxiety agents or 'minor' tranquillizers (e.g. chlordiazepoxide and diazepam), and others such as methaqualone and paraldehyde. They are capable of inducing sedation, relief from anxiety, sleep, general anaesthesia or coma, depending on dose.

The second class of behaviour-depressing drugs contains the 'major' tranquillizers or antipsychotic drugs, so called because they are used to treat serious psychological disorders such as schizophrenia and mania. They are also often called neuroleptics as they may produce a state of emotional quietness and indifference called neurolepsy. This is the type of effect required for the marmosets.

There are six main groups of major tranquillizers :

- 1) Phenothiazines e.g. chlorpromazine, fluphenazine, perphenazine.
- 2) Rauwolfia alkaloids e.g. reserpine.
- 3) Thioxanthine derivatives e.g. flupenthixol.
- 4) Butyrophenones e.g. haloperidol.
- 5) Diphenylbutyl piperidines e.g. pimozide.
- 6) A miscellaneous group including chlormezanone and hydroxyzine.

They are used to relieve symptoms of psychosis (usually schizophrenia) and induce a behavioural state characterized by psychomotor slowing, emotional quieting and an indifference to external stimuli (Julien, 1975; Parish, 1976).

It was decided to exclude sedatives and concentrate on testing tranquillizers as it would appear from the above, and was suggested by Dr. S.W. Holmes of Roche Products Ltd., Welwyn Garden City, Herts., and Dr. R.M. Ridley of the Clinical Research Centre, Harrow, Middlesex, that sedatives would merely sedate the animals, i.e. make them sleepy,

without having very much effect on their social behaviour as such (see also Julien, 1975; Kraemer and McKinney, 1979). Large doses of tranquillizers may produce sedation but this differs from that produced by sedatives in that the subject is easily roused. In general, tranquillizers produce a calming effect without affecting alertness or inducing sleep. They do not depress central nervous system function when administered in therapeutic doses. Their main effect is to reduce the intensity of emotional reactions (Aleksandrowicz, 1974).

It has recently been suggested that amphetamine in low doses can depress social interaction by causing the drugged animal to behave inappropriately. Ridley (1979) and Scraggs and Ridley (1978; 1979) have shown this for common marmosets, and Schiørring (1979) and Schiørring and Hecht (1979) for vervet monkeys. A decrease in social behaviour after amphetamine treatment has also been found to occur in rhesus macaques (Alexander and Isaac, 1965; Haber et al, 1977), and in rats (Cole, 1967; Ellison et al, 1978). Wilson et al (1981) found that 1 mg/kg of amphetamine in stump-tail macaques (Macaca arctoides) produced quiet avoidance, fleeing behaviours, a reduction in social proximity and the elimination of social grooming. However, Houser (1975) reports that for squirrel monkeys (Saimiri sciureus) general 'activity', that is movements recorded by an activity cage, may increase with small doses of amphetamine (0.5 - 1 mg/kg), but then decrease below baseline level after withdrawal of the drug.

A preliminary check through the Monthly Index of Medical Specialities (MIMS), volume 22, number 3, suggested a list of potentially long-acting tranquillizing drugs which could usefully be tested as agents in the reduction of social interaction. The following, together with amphetamine, were obtained from their manufacturers :

(Unless otherwise stated, the information given below is taken from the

following references : Blacow, 1972; MIMS volume 22 number 3; Parish, 1976; Squibb, 1978; Windholz, 1976.)

1) DEPIXOL - flupenthixol decanoate.

Kindly supplied by Lundbeck Ltd., Lundbeck House, Hastings Street, Luton, Beds.

A psychotropic neuroleptic prescribed for psychoses, schizophrenia except the manic phase, and hyperactivity. It may occasionally cause insomnia. Flupenthixol, chemically designated 4-(3-(2-(trifluoromethyl)-9H-thioxanthen-9-ylidene)propyl)-1-piperazine-ethanol, is a substance related to, and with similar effects as, fluphenazine (see below for details). However it is a thioxanthine derivative whose antipsychotic activity is generally less potent than that of phenothiazine derivatives. Figure 5.1 shows the chemical structure.

2) HEMINEVRIN - as crystalline chlormethiazole edisylate.

Kindly supplied by Astra Pharmaceuticals Ltd., St. Peter's House, 2 Bricket Road, St. Albans, Herts.

A sedative-tranquillizer-anticonvulsant prescribed for psychomotor agitation, tension and anxiety, daytime sedation in senile psychosis, confusional states, delirium, sleep disturbances and withdrawal symptoms in alcoholism. It is the ethanedisulphonate of chlormethiazole, 5-(2-chloroethyl)-4-methylthiazole. The chemical structure is shown in figure 5.2. Side-effects include headache, nausea, vomiting, sneezing and dizziness. Drug dependence may quickly develop.

3) REDEPTIN - as crystalline fluspirilene.

Kindly supplied by Janssen Pharmaceutica, 2340 Beerse, Belgium, through the arrangements of Smith Kline and French Laboratories Ltd., Welwyn Garden City, Herts.

Figure 5.1

Chemical structure of flupenthixol

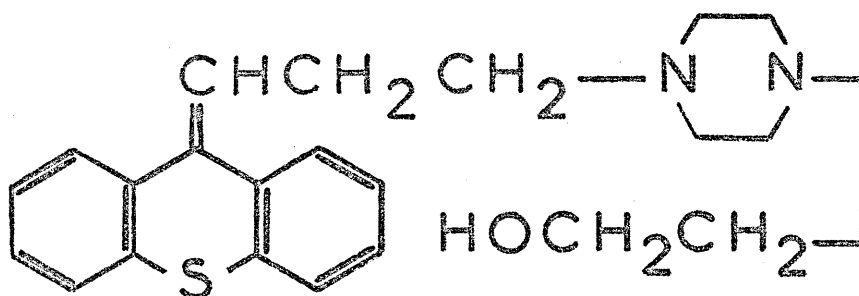


Figure 5.2

Chemical structure of chlormethiazole edisylate

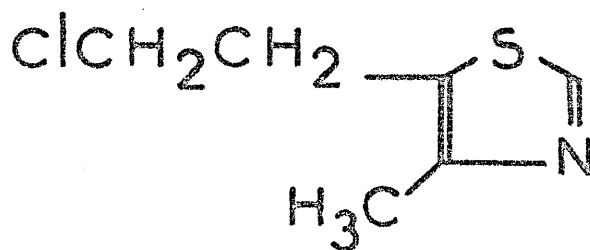
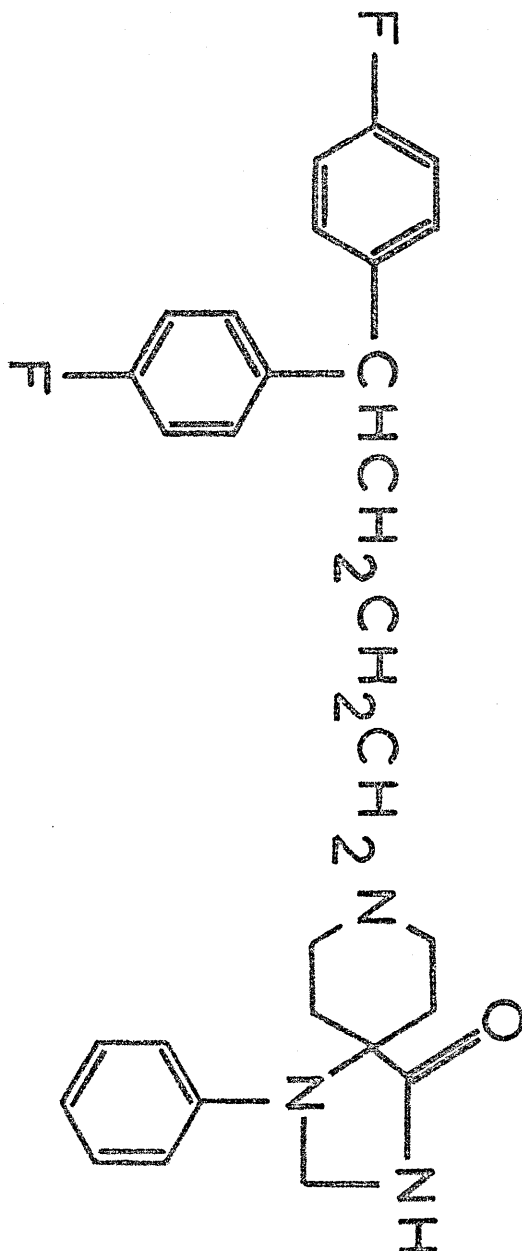


Figure 5.3

Chemical structure of fluspirilene



A long-acting parenteral neuroleptic prescribed for schizophrenia. The mean duration of action of fluspirilene in man is five to seven days (Uchtenhagen and Heimann, 1973). The chemical structure is shown in figure 5.3 and can be written as 8(4,4-bis(4-fluorophenyl)butyl)-1-phenyl-1,3,8-triazaspiro(4,5)decan-4-one. Adverse effects include Parkinsonism and dyskinesia (severe involuntary movements) which may develop in the first 48 hours. The drug may also cause tremor, salivation, nausea, vomiting, drowsiness, insomnia, excitement, anxiety, headache, sweating, blurred vision, dizziness, fall in blood pressure and skin rash.

4) LARGACTIL SYRUP and INJECTION - chlorpromazine hydrochloride.
Kindly supplied by May and Baker Ltd., Dagenham, Essex.

Chlorpromazine was the first major tranquillizer to be discovered and made commercially available, in 1952, and is still prescribed for central nervous system disturbances requiring sedation, and for premedication, induced hypothermia, emesis, schizophrenia and affective disorders. It is used in the alleviation of anxiety, tension and agitation in psychoneurotic and psychotic patients. The patient becomes apathetic, drowsy and occasionally euphoric. This calming effect is of value in manic-depressives, aggressive and hostile patients, and in senile agitation and behaviour disorders in children.

Chlorpromazine is a phenothiazine derivative, 2-chloro-10(3-dimethylamino-n-propyl)phenothiazine. Its chemical structure is shown in figure 5.6. It induces psychomotor slowing, indifference to sensory stimuli, emotional quieting and reduction in initiative without producing excessive sedation and without causing dependence or tolerance. The effects are probably due to drug-induced blockade of dopamine receptors in the limbic system of the brain (Julien, 1975).

The drug may cause dryness of mouth, pallor, dizziness, headache, heartburn, constipation, polyuria, tiredness and weakness, lowering of body temperature, insomnia, skin rashes, vasodilation and fall in blood pressure, tachycardia and reduced gastric secretions. It sometimes produces severe blood dyscrasias, and Parkinsonism at high doses. Although chlorpromazine is generally prescribed as a short-acting substance, it has been found to have a tranquillizing effect for up to six months in man (Goodman and Gilman, 1970).

Largactil syrup was obtained along with the injection form of the drug, but it was decided not to use it as for effective administration it has to be passed down a blue-line infant's feeding tube which is inserted via the mouth down the oesophagus and into the stomach. This would undoubtedly prove a more traumatic experience for these nervous animals and involve a longer period of handling than a simple injection. Observation of this procedure at Roche Products Ltd., Welwyn Garden City, confirmed this view.

5) MODECATE - fluphenazine decanoate.

6) MODITEN ENANTHATE - fluphenazine enanthate.

Both kindly supplied by E.R. Squibb and Sons Ltd., Squibb House, 141/149 Staines Road, Hounslow. Middlesex.

These drugs are tranquillizers prescribed for maintenance treatment of psychotic disorders, particularly schizophrenia. They are used for the relief of anxiety and tension in neuroses and mild emotional disturbances, and in the control of post-operative nausea and vomiting. They also form part of the treatment for acute mania, psychogeriatrics with dementia or depression, senile paraphrenia, paranoia, amphetamine addiction and alcoholism.

Fluphenazine hydrochloride is a phenothiazine derivative with

Figure 5.4

Chemical structure of fluphenazine enanthate

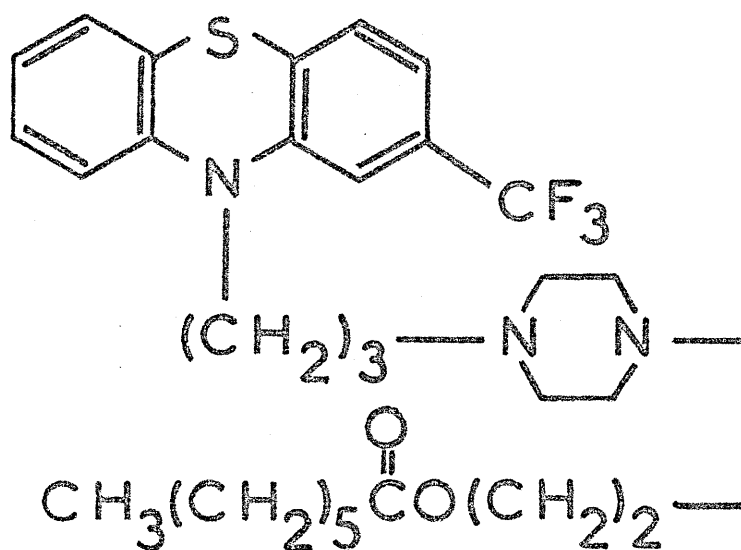
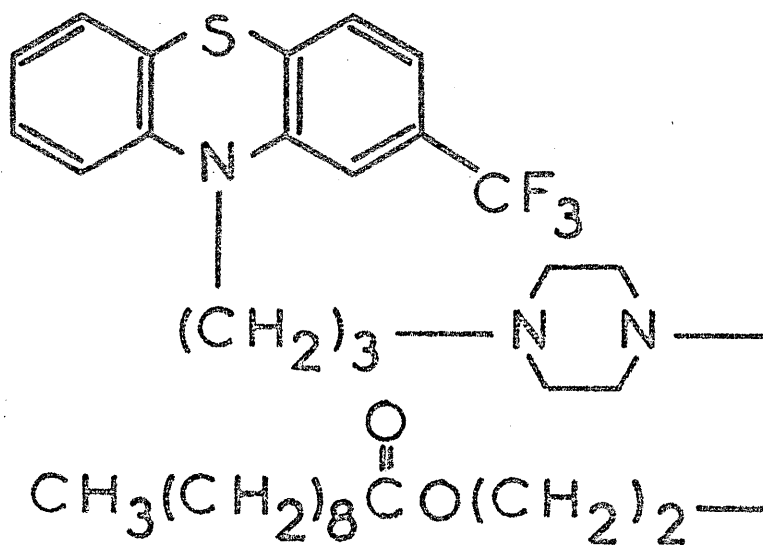


Figure 5.5

Chemical structure of fluphenazine decanoate



a piperazine side-chain; 4-(3-(2-(trifluoromethyl)-10-phenothiazinyl)-propyl)-1-piperazineethanol dihydrochloride. Long acting intramuscular injections of fluphenazine are made by substituting an ester on the piperazine side-chain and dissolving in a sesame oil vehicle. Moditen enanthate is the heptanoic acid ester of fluphenazine, and Modecate is the decanoic acid ester. The chemical structure of these drugs is shown in figures 5.4 and 5.5. Each millilitre of Moditen enanthate consists of 25 mg of fluphenazine enanthate in sesame oil with 1.5% benzyl alcohol as a preservative. Each millilitre of Modecate is 25 mg of fluphenazine decanoate in sesame oil with 1.2% benzyl alcohol as a preservative.

During the first few days after injection of either Modecate or Moditen enanthate the drug is stored at the injection site. Here it is metabolised to free fluphenazine, fluphenazine sulphoxide and other unidentified metabolites. These are transferred to other sites where additional metabolism occurs, and other depots are formed. Small amounts are gradually released and enter the brain almost exclusively as fluphenazine, with possibly some fluphenazine enanthate or decanoate. Here it is rapidly hydrolysed, however the depots provide sufficient amounts to maintain brain levels of fluphenazine which exert a pharmacological effect for three to six weeks in man. Phenothiazine derivatives such as fluphenazine are suggested to act on the hypothalamus. They are believed to depress various components of the mesodiencephalic activating system, which is involved in the control of basal metabolism and body temperature, wakefulness, vasomotor tone, emesis and hormonal balance (Craver, 1965). However, the site and mode of action is not entirely clear. Research into the metabolism of fluphenazine using animals is described in section 5.2).

The actions and uses of fluphenazine are very similar to chlorpromazine (see above) but fluphenazine has the advantages of

greater tranquillizing action and less sedative effects, and a longer duration of action. For fluphenazine itself, Modecate has a longer duration of action than Moditen enanthate. For example in rats, drug-induced inhibition of the conditioned avoidance response drops to 25% after 16 days in the case of fluphenazine enanthate but not until 50 - 55 days after injection of fluphenazine decanoate (Ebert and Hess, 1965). In man, clinical trials have shown Modecate to be effective for about 50% longer than Moditen enanthate, and to cause fewer and less severe extrapyramidal reactions.

In therapeutic doses fluphenazine exerts little effect on the autonomic nervous and cardiovascular systems and adverse side-effects are uncommon. However it may cause hypothermic reactions in subnormal patients with brain damage, and at higher doses is likely to lead to extrapyramidal dysfunction, particularly dystonic reactions and akathisia. These reactions often diminish with repeated injections and can be controlled by anti-Parkinsonism drugs or anti-histamines.

7) AMPHETAMINE - d-amphetamine sulphate.

Acquired through M.W. Smith, MA, MVSc, MRCVS, DTVM, Animal House, New Addenbrookes Hospital Site, Hills Road, Cambridge.

Amphetamine is a sympathomimetic agent with pronounced stimulant effect on the central nervous system, having both α and β adrenergic activity (Burn, 1975). It produces increased activity and mental alertness, lifts mood, diminishes any sense of fatigue, and produces wakefulness. It is also an anorectic agent, depressing appetite or the sensation of hunger. Amphetamine was used widely in the treatment of narcolepsy, postencephalitic Parkinsonism and, together with other agents, epilepsy, chronic alcoholism and poisoning by depressant drugs. It has also been used for lifting mild depressive neuroses and

Figure 5.6

Chemical structure of chlorpromazine hydrochloride

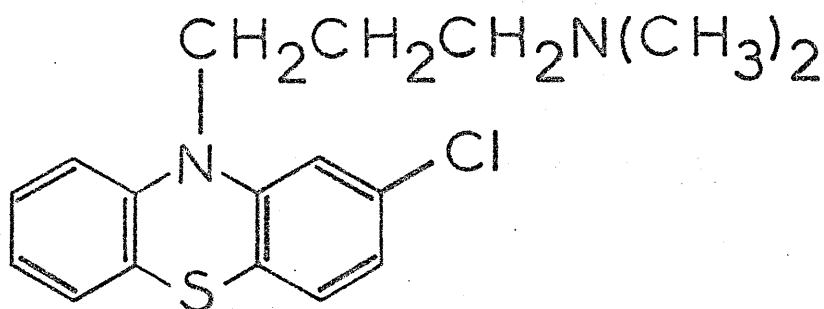
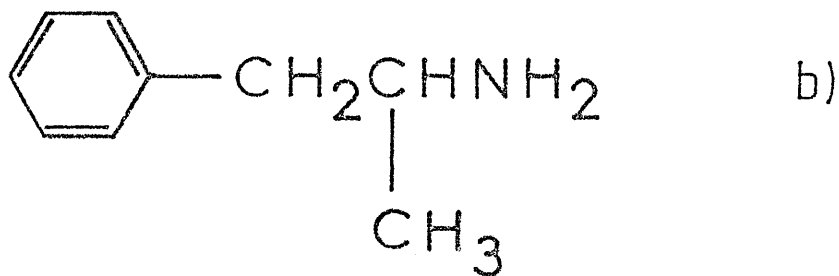
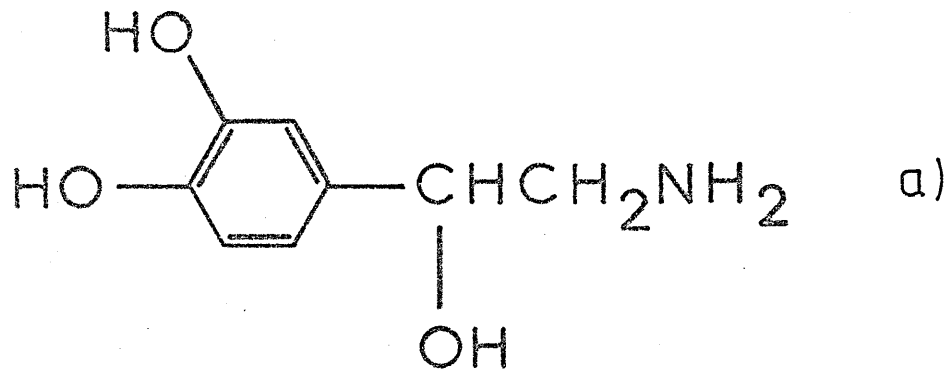


Figure 5.7

Chemical structure of a) amphetamine b) noradrenalin



orthostatic hypotension, and for the treatment of some types of obesity, urinary incontinence and nocturnal enuresis, and behavioural hyperkinesias in children. However its clinical use has greatly decreased due to its potential for abuse and high risk of dependence and tolerance.

Amphetamine appears to relieve depression and induce behavioural stimulation by its ability to increase the amount of noradrenalin at the synapse, releasing it from its presynaptic bound state. It can also block the uptake of noradrenalin as the two molecules are structurally closely related (see figure 5.7). Amphetamine is therefore thought to mimic and potentiate the synaptic action of noradrenalin in the central nervous system and in the rest of the body, by both increasing the release of noradrenalin and by directly stimulating postsynaptic noradrenalin receptors. This bears out the noradrenalin hypothesis of mania and depression whereby low levels of the substance are associated with depression, normal levels with normal behaviour, a slight excess with behavioural stimulation, and a great excess with mania (Rubin, 1978; Julien, 1975).

Side-effects of amphetamine use include headaches, insomnia, dryness of mouth, agitation and restlessness, tremor, anorexia and constipation. With high doses blood pressure is increased and tachycardia, anginal pain or cardiac arrhythmias may occur, as well as fatigue, mental depression, fever, hypotension, respiratory failure, disorientation, hallucinations, convulsions and coma.

5.4) DRUG TESTS.

In order to test the effects of the sample drugs on marmoset interactive behaviour, it was necessary to measure each subject animal's

social activity level before, during and after drug administration. Since the animal room used for these tests (room 3) had no computer facility, observations were restricted to frequencies of occurrence of various behaviours which could be rapidly noted down on a check sheet. This ruled out the inevitable errors involved in trying to obtain durations of behaviours using a stopwatch or clock, and in any case it was felt that differences in frequencies would be quite sufficient for indicating the relative extent of drug effects in these preliminary tests. More exact observations involving durations would be carried out when the chosen drug was actually used in the second part of the study.

To measure social activity level, a series of behaviours were chosen for recording which would be representative of social interaction between animals. These social interaction 'markers' were as follows :

- 1) Drugged monkey approaches cagemate.
- 2) Drugged monkey leaves cagemate.
- 3) Cagemate approaches drugged monkey.
- 4) Cagemate leaves drugged monkey.
- 5) Drugged monkey grooms cagemate.
- 6) Cagemate grooms drugged monkey.
- 7) Drugged monkey successfully initiates playbout.
- 8) Drugged monkey unsuccessfully initiates playbout.
- 9) Cagemate successfully initiates playbout.
- 10) Cagemate unsuccessfully initiates playbout.
- 11) Drugged monkey ignores approach of cagemate.
- 12) Contact between drugged monkey and cagemate.

For explanations of behaviour categories refer to chapter 3. Each time one of these markers occurred during the observation period the event was marked on a score sheet (see appendix 1 for example of score sheet). Qualitative notes of any unusual or otherwise noticeable behaviours

were also made.

The animals used for the preliminary drug tests were adolescents and subadults aged between 48 and 65 weeks. These were housed in pairs (usually pairs of twins) in cages in room 3 away from the family group cages in room 2 at the time these tests were carried out. Chapter 2 contains a description of room 3. The animals were moved out from their own familys' cages at the age of ten months to prevent overcrowding, and as they were not being used in any other projects were free to be used as subjects for drug testing. All family groups were already being observed and thus were not available for testing.

As the observation windows looking into room 3 were not of one-way glass, watches had to be carried out with the observer in complete darkness looking through a small aperture in the black curtaining covering the windows, and using an illuminated clipboard to hold the score sheets. In this way, the observer was still able to see the monkeys without them being aware of being watched.

Before each observation session started the subject's cage was moved so that it was directly in front of the observation window, and the door to the nestbox was closed to prevent the animals disappearing from view during the watch.

Observation periods were of 30 minutes each. This watch length was decided upon after a pre-test watch during which frequencies of approaching and leaving (the most frequently exhibited behaviours) by both members of a pair of monkeys were noted over increasingly larger time intervals from five minutes to 40 minutes. The results appear in table 5.1. A long enough watch was defined as one where, for an additional five minutes of observation time, the percentage change in frequency per minute of the four behaviours recorded was 5% or less. This gave a watch length of 30 minutes for the preliminary drugs tests.

Table 5.1

Pre-test watch : Frequencies of approaching and leaving over 5 minute intervals (cumulative scores).

A, B = Pair of monkeys observed.

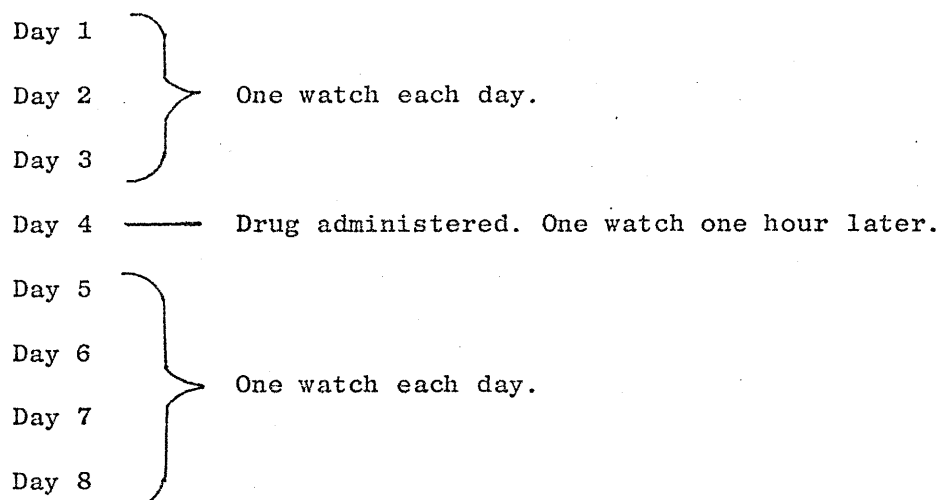
		Minutes since start of watch							
		5	10	15	20	25	30	35	40
<u>A approaches B</u>									
Frequency per minute (N)		1.40	1.10	0.87	0.75	0.60	0.57	0.60	0.57
% change between time intervals (%)		21.40	20.90	13.80	20.00	5.00	5.00	5.00	5.00
<u>A leaves B</u>									
N		1.20	1.00	0.80	0.70	0.60	0.60	0.57	0.55
%		16.70	20.00	12.5	14.30	0.00	0.50	0.50	0.50
<u>B approaches A</u>									
N		0.60	0.50	0.47	0.40	0.36	0.40	0.40	0.42
%		16.70	6.00	14.90	10.00	11.10	0.00	0.40	0.40
<u>B leaves A</u>									
N		0.80	0.60	0.53	0.45	0.36	0.57	0.37	0.37
%		25.00	11.70	15.10	20.00	2.80	0.00	0.00	0.00

The thirteen drug tests lasted eight days (except four of seven days) and consisted of the schedule shown in figure 5.8. The watches on the first three days were to give baseline levels of the measures taken. The watch on the day of drug administration and on the following four days would show any effect the drug (plus injection procedure) had on the animal's behaviour. (The four seven day tests had three rather than four post-drug watches.) Watches were not continued over any longer time period since the behavioural effect was only required to last for four days, and these tests had to be fitted in between observations for Part I. For most drugs measures were back to 'normal', i.e. pre-drug values, by the fourth day after injection so longer tests were not necessary. A fortnight free of drug administration was allowed for complete recovery of normal behaviour between tests on any one pair of monkeys, though usually one week was sufficient for the animals to resume the relative approach and leave frequencies they had shown before testing. Six individual monkeys were tested with drugs. Three animals were dosed with (on different occasions) three different drugs each, two animals with two different drugs each, and two animals each with one type of drug.

On day four of each test, the experimental animal was caught and weighed accurately on a Mettler PK 16 electric balance using a small wire mesh weighing cage in order to determine the correct amount of drug solution to be administered. At the same time it was marked with picric acid solution on the eartufts to ensure complete confidence in identification of individuals during the watches since in room 3 the level of illumination was lower than in the other rooms used for observations, and so facial differences were less clear. The animal was then drugged.

In order to administer the drug, the subject was held down

Figure 5.8 Preliminary drugs test schedule.



using thick leather gloves and given a piece of fruit to occupy it. When the animal had relaxed sufficiently for easy penetration of the needle the drug was injected into either the right or left thigh muscle using a 23 gauge needle and a glass Gillette 1ml syringe. This procedure was carried out in low lighting conditions, partly as the monkeys tended to remain calmer in dim light and partly because some of the drugs were photosensitive (i.e. Modecate, Moditen enanthate, Largactil and Depixol).

For the initial testing, a low dose equivalent to that of a human test dose (taken from MIMS volume 22 number 3) was used for each drug. This was then increased for further tests where the results indicated a possible useful effect. All drugs were injected intramuscularly into the thigh and as these are small animals (adults around 450 grams) it is desirable that the injection volume should be no more than 0.1 - 0.2 mls (Ridley, pers. comm.; Scraggs and Ridley, 1978). To achieve this, all drug samples which were already in the form of oily injections had to be diluted with sterile arachis oil so that the required dose of drug could be obtained in the minimum volume of oil.

Table 5.2

Drug doses and dilutions.

DRUG	DOSE mg/kg	DILUENT	SOLVENT	SOLUTION CONCENTRATION mg/ml
Depixol	0.3	arachis oil		1.0
"	0.5	"		"
Modecate	0.18	"		0.5
"	0.25	"		"
Moditen enanthate	0.18	"		"
Largactil injection	0.35	saline (0.85% NaCl)		1.0
Amphetamine	1.0		saline	6.0
Fluspirilene	0.028		chloroform/ arachis oil	0.1
Chlormethiazole edisylate	3.6		absolute alc. /arachis oil	10.0

Fluspirilene

10mg crystals dissolved in 10mls chloroform.

This mixed with 100mls arachis oil.

Boiled gently for 10 minutes on hotplate with magnetic stirrer.

Chlormethiazole edisylate

100mg crystals added to 5mls absolute alcohol.

This mixed with 10mls arachis oil.

Boiled gently for 10 minutes on hotplate with magnetic stirrer.

Table 5.3

Preliminary Drugs Tests.

TEST NO.	SUBJECT sex weight	age/wks	DRUG	INJECTION VOLUME/mls	DOSE/ mg/kg
1	♂ 341.0	48	Depixol	0.10	0.3
2	♂ 344.4	49	Depixol	0.17	0.5
3	♂ 368.6	57	Largactil	0.13	0.35
4	♀ 417.9	57	Fluspirilene	0.12	0.028
5	♂ 349.7	59	Chlormethiazole edisylate	0.12	3.6
6	♂ 344.3	64	Amphetamine	0.06	1.0
7	♂ 399.5	55	Moditen enanthate	0.14	0.18
8	♂ 332.4	56	Modecate	0.12	0.18
9	♂ 365.7	61	Modecate	0.18	0.25
10	♂ 423.2	61	Modecate	0.21	0.25
11	♂ 360.8	62	Modecate	0.18	0.25
12	♀ 423.7	64	Modecate	0.21	0.25
13	♀ 329.9	65	Modecate	0.16	0.25

Largactil was diluted with saline. The two crystalline tranquillizers, fluspirilene and chlormethiazole edisylate, were made up by first dissolving the drug in chloroform or absolute alcohol, mixing this with arachis oil and then boiling off the initial solvent. The d-amphetamine sulphate sample was dissolved in sterile saline. Doses used and dilution procedures are given in table 5.2.

In all, thirteen preliminary drugs tests were carried out, one on each of the seven sample drugs at low doses, a second on Depixol at a higher dose, and five more on Modecate at a higher dose. The details are given in table 5.3.

The drug tests were carried out while I and the technicians involved held a Home Office license to perform experiments on living animals with permission to use primates under Certificate A1.

5.5) RESULTS

The results for the thirteen preliminary drugs tests (P.D.T.'s) are given below in the form of graphs of the measure $\%AP.DM - \%LV.DM$, that is, the percentage of all approaches attributable to the drugged monkey (DM) minus the percentage of all leavings that were made by the drugged monkey. See chapter 3 for further discussion of this measure. In the case of these tests, all changes in behaviour were in the same direction, so a decrease in $\%AP.DM - \%LV.DM$ means the drugged animal approached less and left more in every case. The other possible combinations (e.g. an increase in approaches but a greater increase in leavings) do not apply here. For this reason, individual $\%AP.DM$ and $\%LV.DM$ scores are not given.

During the tests the only behaviours to be performed in any number were approaches and leaves. The other social interaction markers

rarely occurred during the test observation periods, appearing with much lower frequencies than for animals watched during Part I of the study. Table 5.4 compares these frequencies, taken before animals were drugged, with data available from Part I. Excluding approaches and leavings, it can be seen that all behaviours except 'subject is groomed' occur more often in the Part I animals than in the drugs test animals, and this is highly significant ($p \leq 0.01$, two-tailed Mann-Whitney U tests). 'Subject is groomed' occurs slightly more often in drugs test animals but the difference is non-significant.

This could be related to the different social and physical environments in the two animal rooms involved. Individuals used as subjects in Part I were living with their families in the large cages in room 2. Those used in the P.D.T.'s were housed in pairs, usually pairs of twins, in smaller cages in room 3 (see chapter 2 for details). This restriction in physical and social environments in the case of the P.D.T. monkeys could be expected to be associated with a difference in the variety and quantity of many of the behaviours normally exhibited. These effects may be less severe if social restriction is not compounded with environmental restriction. Bajpai (1980) concluded that isolating rhesus monkeys in their natural environmental - i.e. in open door cages on trees in a forest reserve with no other rhesus population, as opposed to restrictive laboratory caging - did not totally obliterate positive social responses even after 18 months of social isolation, though isolates showed less approaching, grooming, proximity and contact with a stimulus animal than did non-isolated controls. 12 months of isolation in a laboratory setting is enough to severely alter social responses (Mitchell, 1968a).

In the case of physical restriction, Castell and Wilson (1971) found that pigtail macaque mothers punished their infants twice as

Table 5.4

Comparison between Preliminary drugs test and Part I behavior frequencies.

Figure are mean frequencies of behaviours per 30 minutes observation time plus or minus standard errors. Probabilities refer to results of two-tailed Mann-Whitney U tests (Siegel, 1956).

Part I data - mean score of 9 subjects aged 22 weeks = 36 watches.

Preliminary drugs test data - mean score of pre-drug watches of 13 tests = 36 watches.

BEHAVIOUR	PART I	PRELIMINARY	
		DRUGS TESTS	PROBABILITY
Subject grooms	0.407 + 0.175	0.114 + 0.268	0.0188
Subject is groomed	0.046 + 0.024	0.143 + 0.072	0.4592
Subject plays	2.046 + 0.281	0.129 + 0.062	0.00006
Contact between pair	0.333 + 0.142	0.229 + 0.101	0.0156
Approaches by subject	4.398 + 0.510	12.314 + 1.125	0.00006
Approaches to subject	3.092 + 0.412	11.328 + 1.091	0.00006
Leaves by subject	3.759 + 0.442	11.414 + 0.871	0.00006
Leaves from subject	3.593 + 0.459	11.328 + 0.948	0.00006

often if housed in smaller cages ($0.7\text{m} \times 0.5\text{m} \times 0.6\text{m}$) rather than larger cages ($1.1\text{m} \times 2.1\text{m} \times 1.1\text{m}$). Infant pigtail macaques housed with their mothers in bare cages were found to show less behaviour oriented towards their environment, less locomotion, less climbing, and less differentiation in manipulation of their mothers than those mother-infant pairs housed in cages containing toys (Jensen et al, 1968a).

As noted above however, the numbers of approaches and leavings occur at a much higher frequency in the preliminary drug tests than during the Part I watches ($p < 0.00006$). This is likely to be because in the smaller cages it is more difficult for the animals to avoid each other, and any general movement around the cage is liable to lead to the monkeys moving towards or away from each other. It would require a positive effort on their part not to approach and leave each other often.

In addition, the differences in behaviour frequencies could at least partly be due to the fact that the subjects in Part I were younger than those used in the drugs tests.

Below and in the graphs which follow are the results for the preliminary drugs tests. In all graphs conventions are as those in figure 5.9.

Test nos. 1 and 2 - DEPIXOL

See figure 5.9. Pre-drug values of %AP.DM - %LV.DM are around zero indicating both animals are playing a role in maintaining proximity between them. However after injection the value drops as the drugged monkey maintains proximity far less and instead avoids interaction by leaving relatively more often. This effect lasts one day at the lower dose (0.3 mg/kg) and two days at the higher (0.5 mg/kg), though in the latter the difference is less marked. In both tests the drugged monkey

tended to ignore its twin's approaches and refuse to sit in contact with it during the watch on the day of injection.

Test no. 3 - LARGACTIL.

See figure 5.10. As with Depixol, pre-drug values of %AP.DM - %LV.DM around zero drop to a negative value on the day of drug administration. In the following three days the effect reverses before dropping back to a normal, or pre-drug, level. Although there was no play or contact between the animals on the drug day, there were three bouts of grooming between them during the observation period, so though the drugged monkey avoided its partner more than usual social interactions were not completely eliminated.

Test no. 4 - FLUSPIRILENE.

See figure 5.11. In this test the subject animal played only a small role in maintaining proximity and initiating interactions normally, i.e. pre-drug administration, and this dropped even lower after injection of the drug. This effect lasted only one day though post-drug values of %AP.DM - %LV.DM were more variable than those pre-drug. This drug appeared to interfere with motor co-ordination as head-shaking (similar to the 'checking' seen with amphetamine) and jerky movements were seen on the drug day. Grooming between the two animals which had been seen during pre-drug watches was not seen again after day 3.

Test no. 5 - CHLORMETHIAZOLE EDISYLATE.

See figure 5.12. Pre-drug values of %AP.DM - %LV.DM range around zero but drop with drug administration to recover by the second day after injection. However by the end of the test (day 8) the measure has begun to drop again. Normal scores for this drug are variable to the

extent that the results of this test are inconclusive.

Test no. 6 - AMPHETAMINE.

See figure 5.13. At the low dose used amphetamine depresses the social interactions of the injected animal. The measure %AP.DM - %LV.DM drops from around zero to a negative value and overall activity is reduced on the day of injection. Small head movements and jerks, called 'checking' (Scraggs and Ridley, 1978) were also seen on this day. On the following days the measure returns to around zero, dropping again on day 7 and rising on day 8.

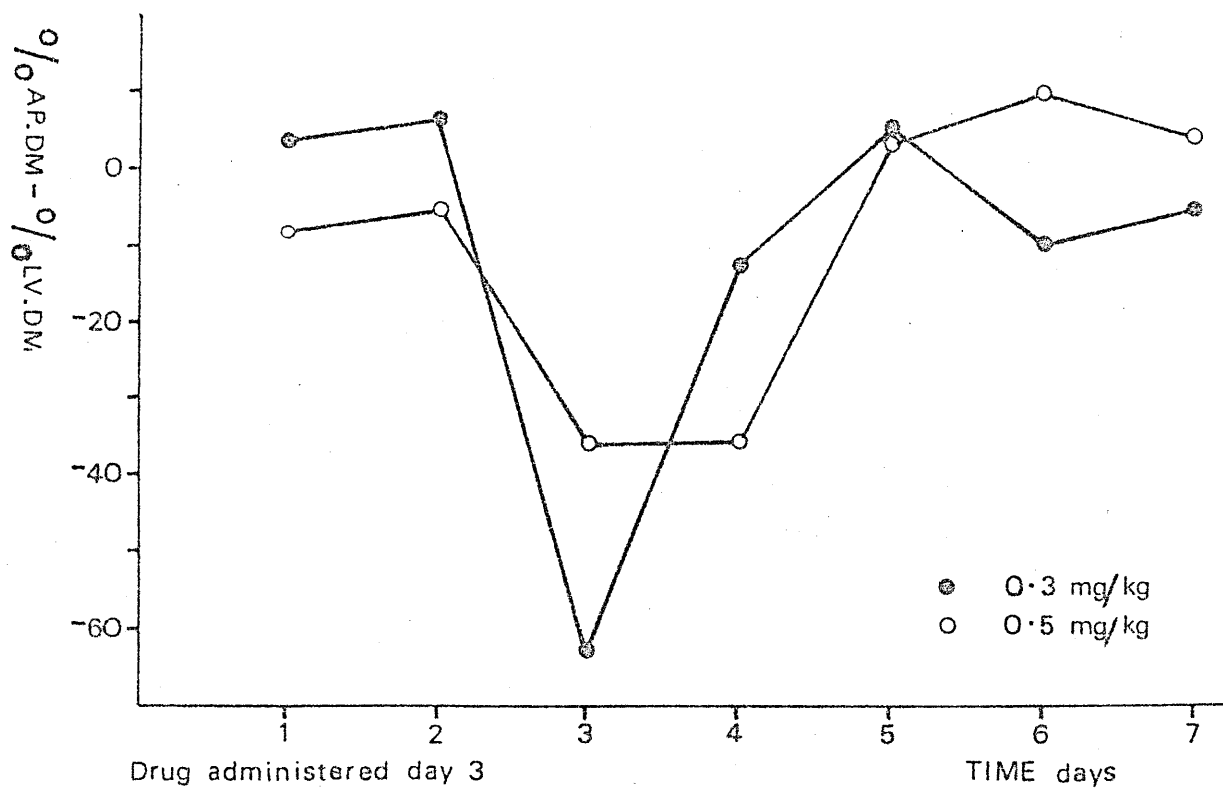
Test no. 7 - MODITEN ENANTHATE.

See figure 5.14. Pre-drug values of %AP.DM - %LV.DM are positive indicating that the animal to be drugged plays the more important part in maintaining proximity between the two. Injection of Moditen enanthate reverses this and %AP.DM - %LV.DM becomes negative. This effect lasts for two days, though suppression of grooming between the monkeys occurred only on the day of drug administration.

Test no. 8 - MODECATE.

See figure 5.15. The results for Modecate are very similar to those for Moditen enanthate, to which it is chemically closely related, however the depression of social interactions lasts for an extra day, the drug being effective for three days at the low test dose used.

FIGURE 5.9 Proximity maintenance by drugged monkey. DEPIXOL P.D.T.'s
(see text)



$\%AP.DM - \%LV.DM$ = percentage of approaches by
drugged monkey minus percentage of leavings by
drugged monkey

FIGURE 5.10 Proximity maintenance by drugged monkey. LARGACTIL P.D.T.

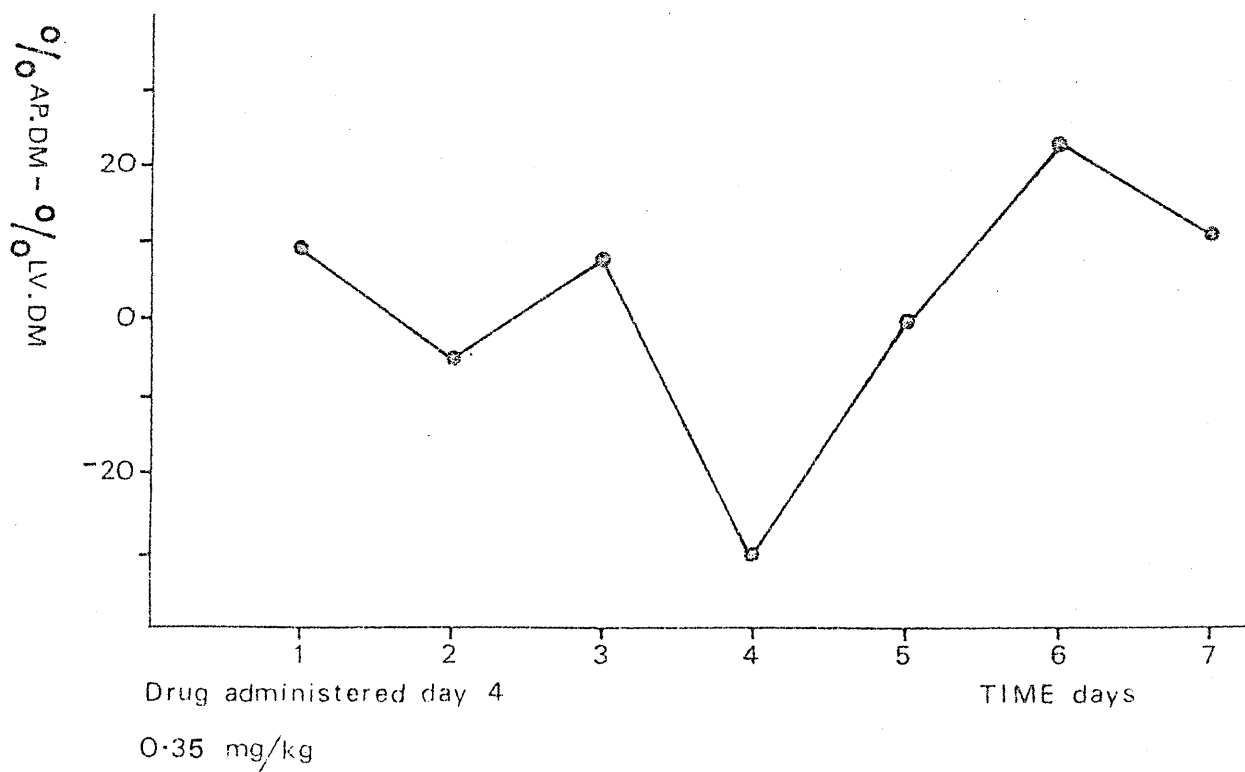


FIGURE 5-11 Proximity maintenance by drugged monkey. FLUSPIRILENE P.D.T.

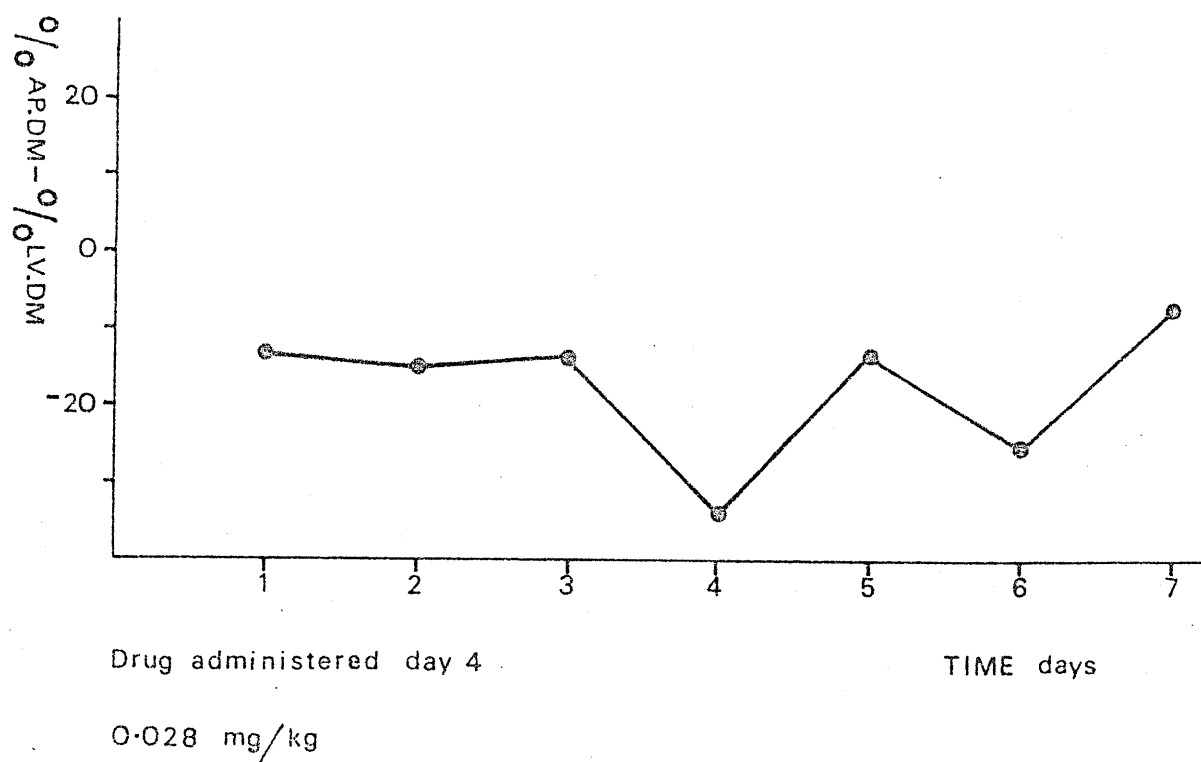


FIGURE 5-12 Proximity maintenance by drugged monkey. CHLORMETHIAZOLE EDISYLATE P.D.T.

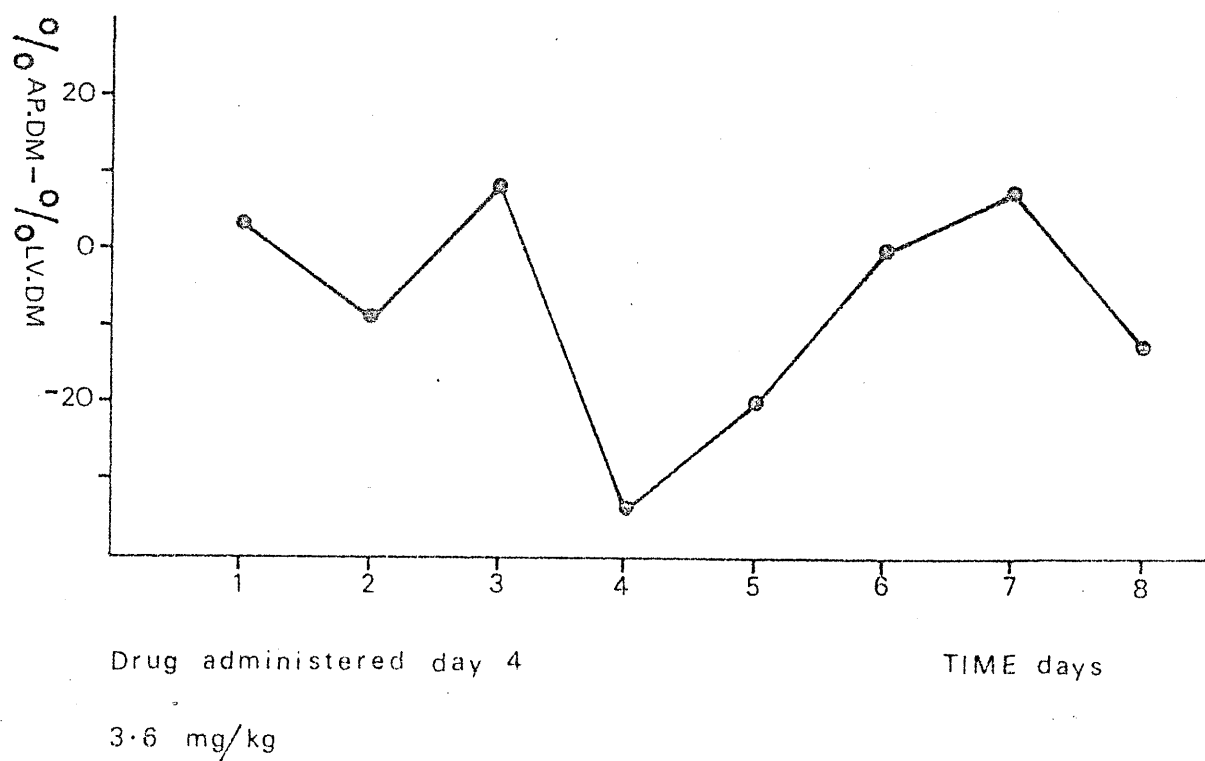


FIGURE 5-13 Proximity maintenance by drugged monkey. AMPHETAMINE
P.D.T.

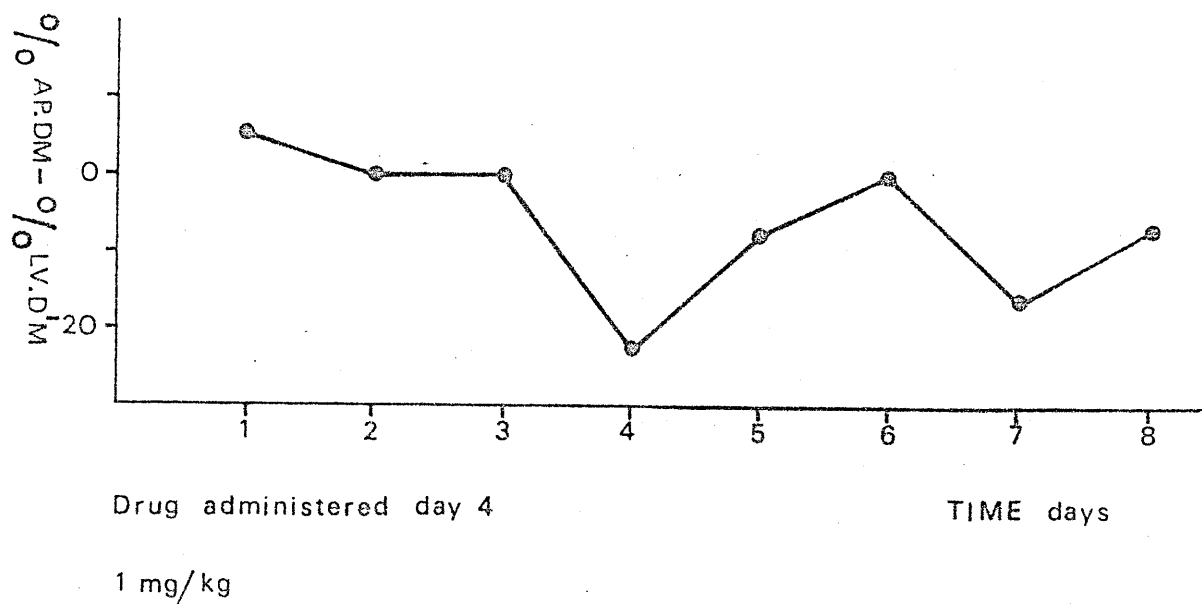


FIGURE 5-14 Proximity maintenance by drugged monkey. MODITEN
ENANTHATE P.D.T.

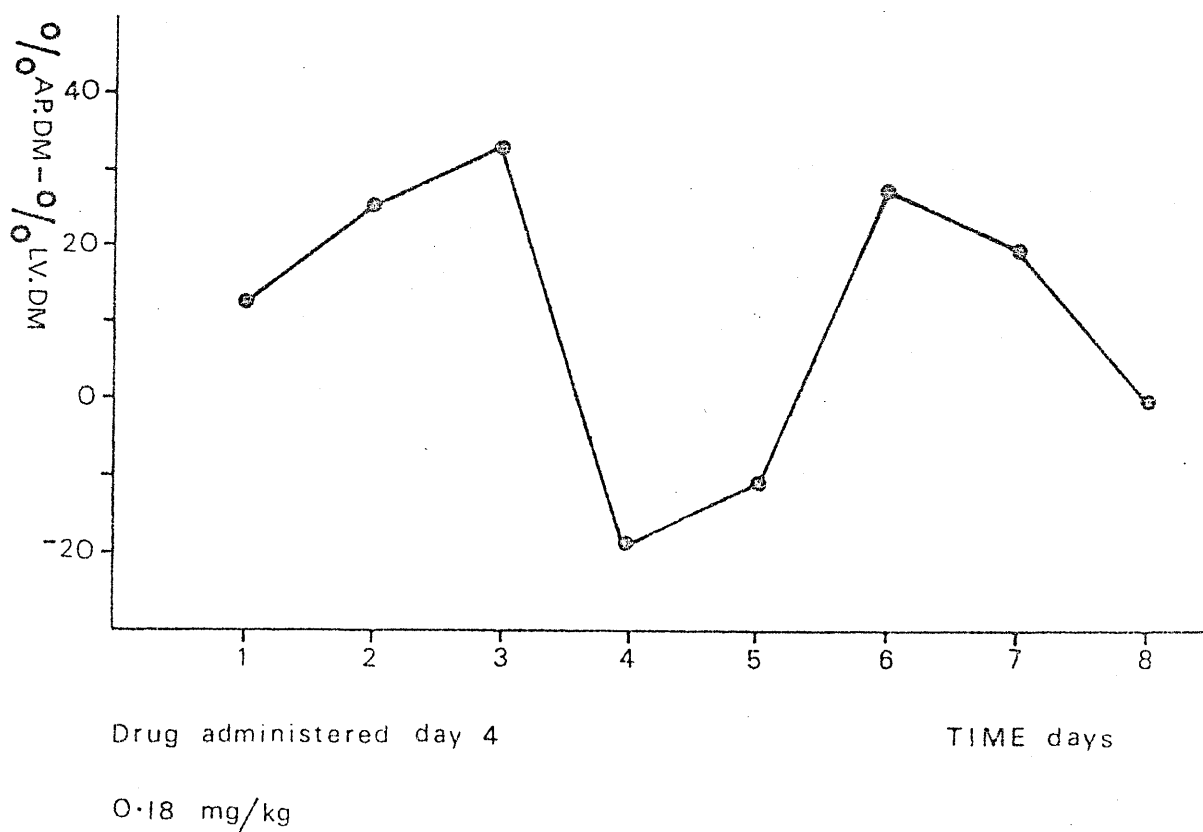


FIGURE 5-15 Proximity maintenance by drugged monkey. MODECATE P.D.T.

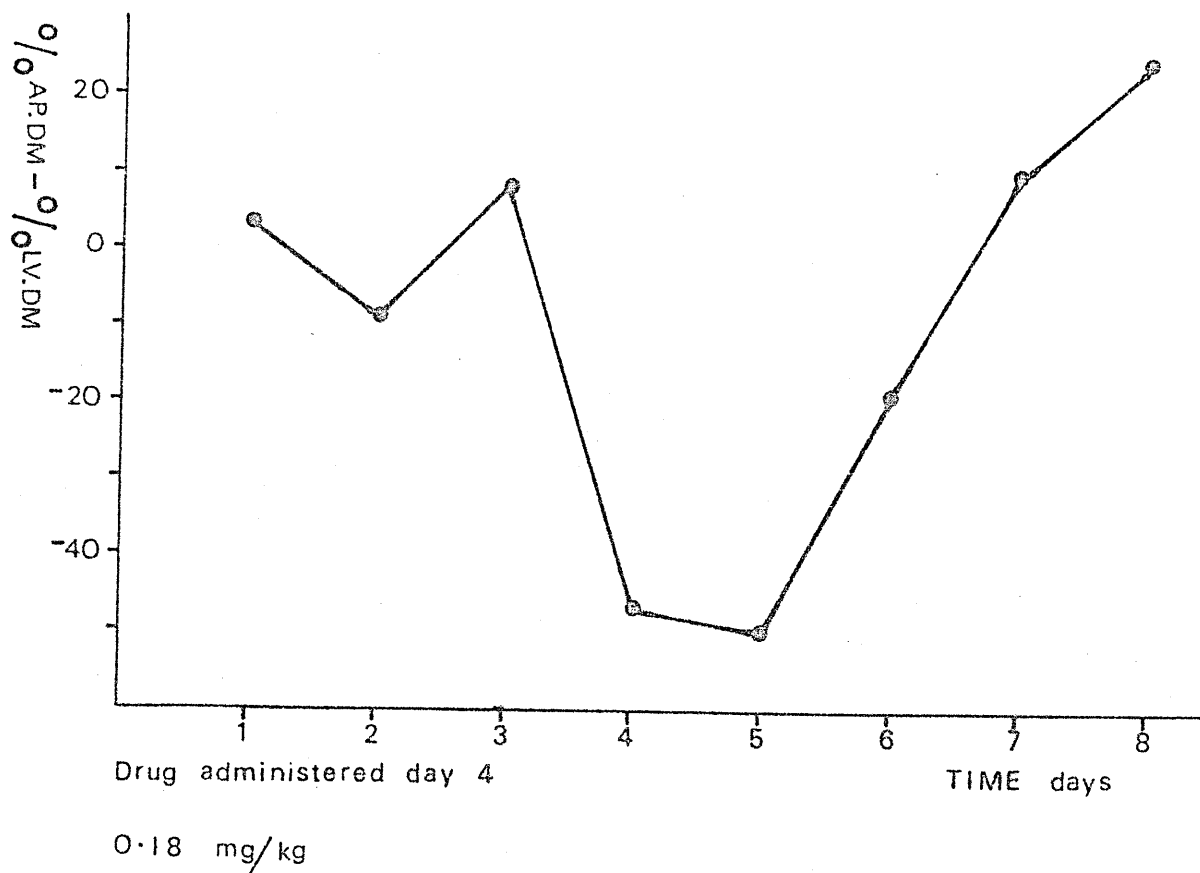
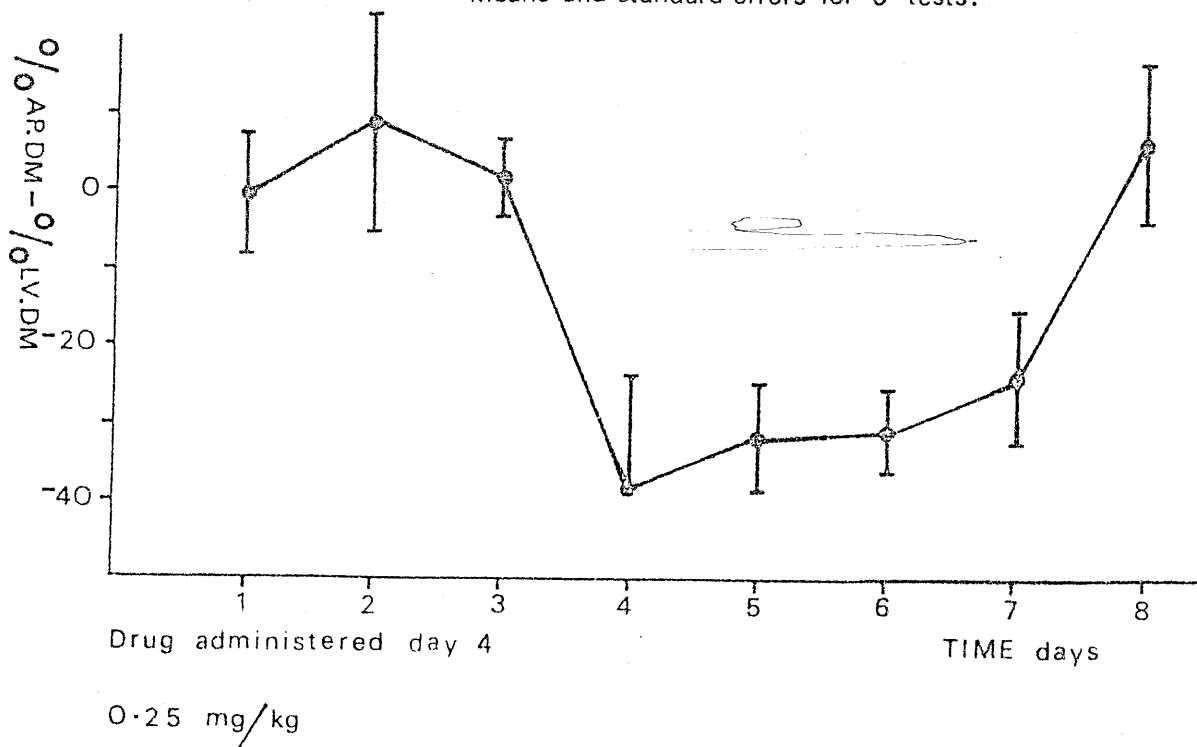


FIGURE 5-16 Mean proximity maintenance by drugged monkeys. MODECATE P.D.T.'s
Means and standard errors for 5 tests.



From the results of the above tests it appeared that Modecate would be the most suitable drug to use. Even at the low dose used in test no. 8 (equivalent to a human test dose) the %AP.DM - %LV.DM score made a large drop on administration of the drug indicating that the drugged animal ceases to be important in the maintenance of proximity and initiation of social interactions. Normal pre-drug values do not re-appear until the third day after injection. In addition to this all other social contact between the two monkeys (allogrooming, playing, huddling) is eliminated. In order to check the reliability of this effect on marmoset social interactions and if possible extend its duration, five further tests were carried out using Modecate at a higher dose, 0.25 mg/kg as opposed to 0.18 mg/kg as in test no. 8. The results of these tests (numbers 9 to 13) are given in figure 5.16 as mean %AP.DM - %LV.DM scores.

As can be seen from figure 5.16, although the drop in responsibility for maintenance of proximity is not as large as in test 8 it is a full four days before normal pre-drug values are re-attained. A reason for the smaller drop is that taking the mean value from several tests tends to iron out any particularly large differences. The largest drop found for Modecate at 0.25 mg/kg was to -83.33, a difference of 77.35 from the mean of the pre-drug values for that test. The equivalent figure from test 8 is -47.06, a difference of only 49.84.

As at the lower dosage, other social contact including huddling and grooming is also eliminated.

The significance of the changes in %AP.DM - %LV.DM between pre-drug, drug, and four post-drug observation periods was assessed by the Friedman two-way analysis of variance test (Siegel, 1956). For $N = 5$ and $k = 6$, $\chi^2 = 17.92$, $p < 0.01$ indicating that the scores obtained are significantly affected by the Modecate treatment.

Since the drugged animals in each test had their eartufts dyed

1.1.0
it might have been expected that more allogrooming would occur in the following observation period as the drugged monkey's cagemate investigated and attempted to remove the dye. The reverse occurred and though the overall frequencies of grooming in any of the watches were too small for any firm conclusions this does back-up the depressant effect of the drug on marmoset social behaviour.

The effects reported for the preliminary drugs tests may not entirely be due to the drugs used, but may be partly an effect of the shock or trauma (though every effort was made to keep this to a minimum) of the procedure of catching and injecting the monkeys. These two possible causes could not be separated out in the present tests, though their relative effects could be discovered by running more tests using placebo (saline or arachis oil vehicle) instead of drug injections. This was felt unnecessary since provided the procedure gave reliable results the precise cause was not required, and time and space did not permit any additional tests.

The results of the preliminary drugs tests indicated that the substance to use to modify infant-caregiver relationships by depressing social interactive behaviour would be the long-acting neuroleptic Modecate, administered by a single intramuscular injection at a dose of 0.25 mg/kg body weight. This would have sufficient effect for a sufficiently long time period to enable predictions based on the model of marmoset infant social development to be tested through a series of watches comparable to those carried out in order to construct the model.

CHAPTER 6 - Modified Infant-Caregiver Relationships

6.1) INTRODUCTION

This chapter investigates the effects on infant-caregiver relationships of altered levels of caregiving brought about by the administration of the neuroleptic drug fluphenazine decanoate (= Modecate, described in chapter 5), and presents the results from Part II of the study. In the first part of the chapter, data will be presented to show the effects of the drug on the behaviour of the drugged caregivers (fathers and siblings). The rest of the chapter is concerned with testing the validity of the predictions made at the end of chapter 4 concerning the behaviour of infants and caregivers, and with a preliminary investigation of the time course of the social behavioural effects of drug administration.

The observation schedule followed and behaviours recorded are identical to those for Part I of the study and are described in chapter 3. The Part II families were living in the same conditions as the Part I animals (see chapter 2).

As described in chapter 5, the drug was administered to fathers and siblings only. Fathers were drugged when the infants were 4 weeks old, i.e. on the first day of that week, such that the fathers were affected by the drug during all of the watches at that age. The age of 4 weeks was chosen since at this age fathers are very important as caregivers to the infant, spending relatively large amounts of time carrying them and grooming them (see data in chapter 4). Similarly, both older siblings were drugged when the infants were 14 weeks old, such that all watches carried out at that age were of infants with drug-affected siblings. The age of 14 weeks was chosen for sibling drug

administration since at this time much of an infant's active behaviour consists of vigorous play with its siblings and relatively little time is spent with the parents. Other major activities at this age tend to be non-social such as resting, sleeping and moving about independently, so that although interactions with siblings do not take up a very large proportion of the infant's time, they are among the most prominent social behaviours at this age (see chapter 4).

Drug administration was carried out between 9.30 am and 10.30 am on the Monday morning of the drug week. The animals were then returned to their families and not disturbed again that week since the pilot studies had shown the drug to be effective for four days (see chapter 5). Observations were commenced one hour after administration to allow time for the drug to take effect and for the animals to return to their normal activities after the disturbance of the capture and temporary removal of the caregivers to be drugged.

All statistical comparisons made between results of Part I and Part II are by two-tailed Mann-Whitney U tests, and comparisons within Part II are by two-tailed randomization tests (Siegel, 1956), both with a 5% significance level.

Following the findings of sections 4.5b) and 4.7), results for sibling 1's and sibling 2's are combined into a single category 'siblings'. For frequency and duration measures, the scores for each pair of siblings (sib 1 and sib 2) are summed, to give for example the percentage of time with siblings, i.e. the total percentage of time with both siblings. This is because it is the total amount of each behaviour that occurs with each category of caregiver that is of interest.

Throughout this chapter, 'Part I' refers to data or animals from the undisturbed first Part of the study (results of which are given in chapter 4), and 'Part II' refers to data or animals from the second

Part where fathers and siblings are drugged at 4 and 14 weeks respectively. Half of the Part II infants had older siblings which had experienced drugged caregivers when they themselves were infants, while half had not. It is however unlikely that this will confound the interpretation of differences between Part I and Part II since the differences are so short-lived (see below section 6.4) and chapter 7).

In chapter 4, the terms 'care' and 'caregiving' were, for the purpose of describing and explaining the caregiving/care-seeking hypothesis, equated with one easily measured activity, namely time on. However 'care' is not a unitary phenomenon but can be defined (if rather loosely) as any activity by one individual which promotes the welfare of another individual (in this case the infant). In the terminology of kin selection theory, care is equivalent to altruism investment (see section 4.9)), i.e. any investment by a caregiver in an individual infant that increases the infant's chance of surviving (and hence reproductive success) at the cost of the caregiver's ability to invest in other infants (Dawkins, 1978; Trivers, 1972 & 1974). By this definition many behaviours occurring between caregiver and infant could become part of the category care. Examples include behaviours which are obviously beneficial to the infant but costly to the caregiver (in terms of time and energy) such as carrying and food-sharing, other behaviours which are presumably less costly to the caregiver such as grooming and contact, and even negative behaviours such as rejections, aggression and ignores when these are used to protect the infant and regulate the growth of its independence. Play is considered by many (e.g. Baldwin & Baldwin, 1974; Chalmers & Locke-Haydon, 1983; Dolhinow & Bishop, 1970; Loizos, 1967; Poirier & Smith, 1974) to have a socializing function and to be of value to the infant as practice for the development of physical and social skills, and as such can also be thought of as a form of care.

This is particularly so when the costs and benefits are unevenly distributed, e.g. when the opportunity for play is provided by an older (and therefore presumably more socialized) animal to an infant.

Though a global definition of care may be valid when discussing the caregiving/care-seeking balance in general terms or with reference to the evolution of behaviours, in specific cases where the balance is being studied it is perhaps more useful to have a tighter definition of care in order that it can be meaningfully measured. It would be exceedingly difficult to measure every aspect of care as defined above and combine the measures in any realistic way. Therefore, in this chapter 'care' will be more closely defined as behaviours which provide the infant with stationary physical contact of some kind, including time on, contact and grooming, since these would afford protection, warmth, security and (in the case of care from the mother) a chance to feed for the infant. Behaviours leading to these states, such as picking up and approaching, will also be included. Some other behaviours (e.g. play) which come under the wider definition of care will be discussed where appropriate, but unless stated to the contrary, the term care as used in the rest of this chapter excludes these behaviours.

6.2) THE EFFECTS OF THE DRUG ON CAREGIVING BEHAVIOUR

As a tranquillizer, fluphenazine decanoate could be expected to reduce caregivers' responsiveness to their infants and therefore reduce the level of care they are prepared to give. The pilot tests also indicated this (see chapter 5), showing that drugged animals tended to avoid interactions with their cagemates.

In this section data are presented which demonstrate the effects of the drug on the drugged animal's behaviour towards the infant. Results

are given separately for fathers and siblings. As noted above, data for drugged versus undrugged caregivers (i.e. Part I versus Part II results) are compared using two-tailed Mann-Whitney U tests.

a) Fathers.

Figures 6.1 to 6.9 compare Part II fathers (drugged when the infants are 4 weeks) with Part I fathers (undrugged controls) in their performance of the following behaviours: Time spent with infant, time spent carrying infant, frequency of picking up infant, time spent grooming infant, time spent in contact with infant, frequency of ignoring infant, absolute and relative frequencies of rejection of infant, amount of aggression shown towards infant, and frequencies of approaching and leaving infant. These behaviours were chosen for comparison as indicators of the father's willingness to show care and attention towards his infant.

When examining the results it is necessary to bear in mind the fact that the siblings of each Part II infant were drugged when the infants were 14 weeks old, so any changes in the father's behaviour around this age could indirectly be related to changes in siblings' behaviour through effects on the social nexus of the infants.

At 2 weeks of age there are no significant differences between the behaviour of Part I and Part II fathers, indicating that the two groups are comparable in the amount of care offered by fathers prior to the drug administration.

Part II fathers spend rather less time with infants (figure 6.1) and less time carrying infants (figure 6.2) at the age at which they are drugged than do Part I fathers, but the differences are small and not significant. Part II fathers also spend slightly more time with infants than Part I fathers at 14 weeks.

Figure 6.1

Mean percentage of time infants spend with their fathers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Probabilities refer to results of two-tailed Mann-Whitney U tests.

*** $p < 0.002$. ** $p < 0.02$. * $p < 0.05$; ns non-significant.

Tests are between data from Part I and Part II at each age.

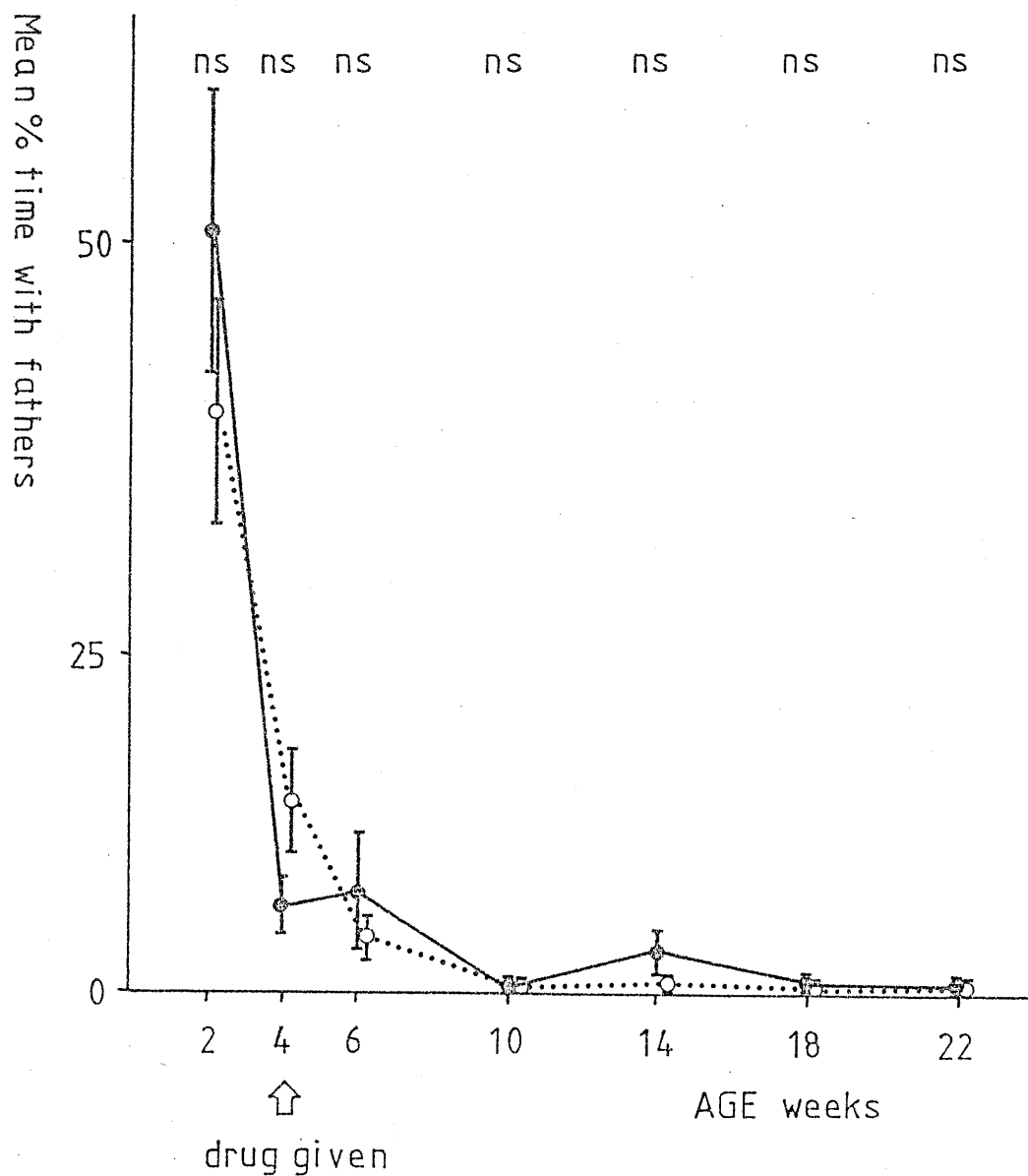
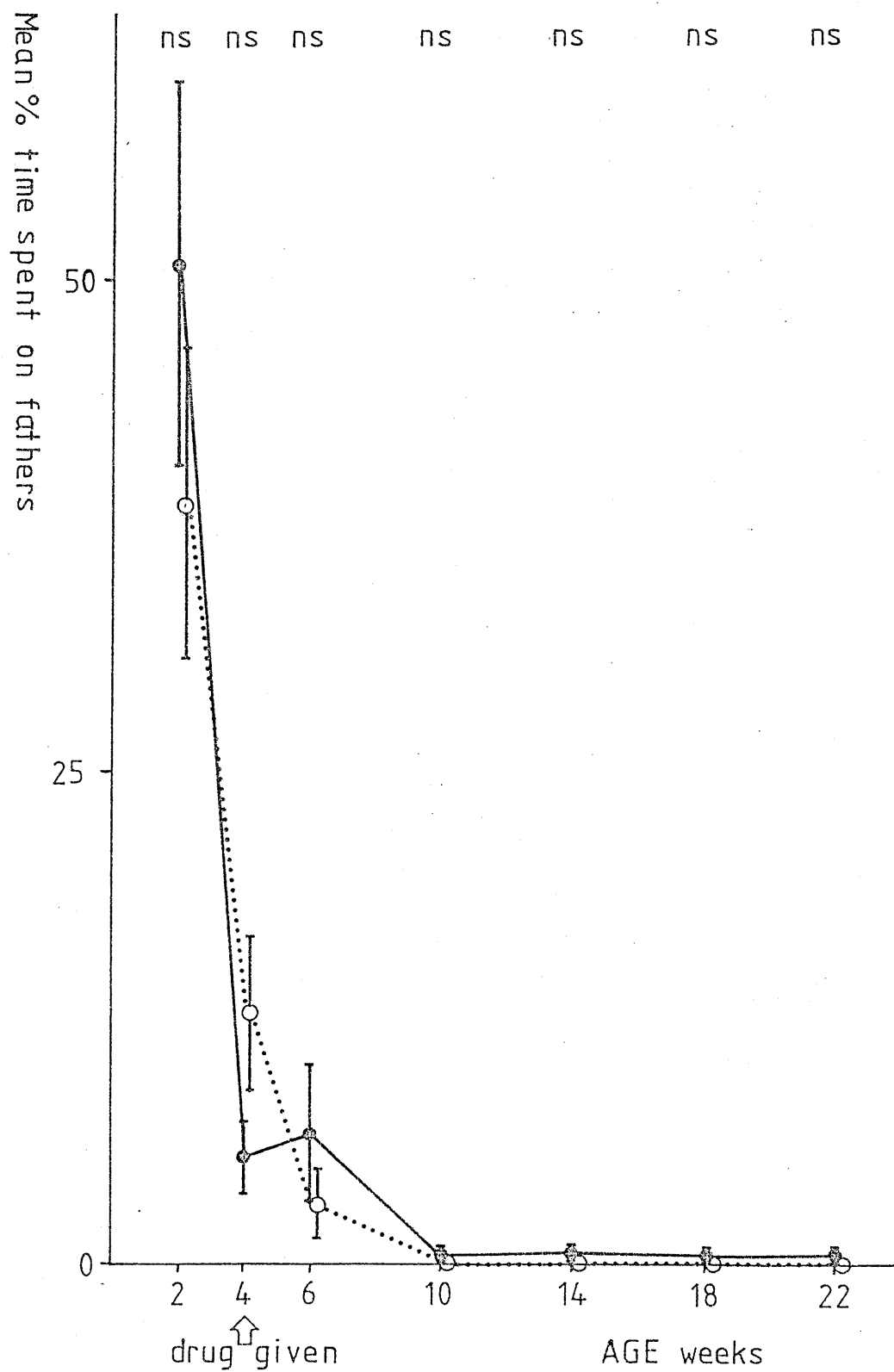


Figure 6.2

Mean percentage of time infants spend on their fathers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.



Part II fathers however, pick up infants significantly less often than Part I fathers at 4 weeks (figure 6.3), and groom infants significantly less often at 4 and 6 weeks (figure 6.4). Since time carrying by Part II fathers is not significantly reduced as compared with Part I fathers but the frequency with which they pick up infants is reduced, this suggests that the bouts of time carrying by Part II fathers are longer. This is confirmed by figure 6.31 in section 6.3b) below which shows that Part II infants do not make more attempts to get on fathers than Part I infants, and hence are not compensating for the fathers' reduced frequency of picking them up.

There are no significant differences between Part II and Part I fathers at any age in the time they spend in contact with infants, in the number of times they ignore infants, in the amount of aggression they show to infants, or in their absolute frequency of rejection of infants (figures 6.5, 6.6, 6.7 and 6.8). Part II fathers do, however, have a significantly lower relative frequency of rejection at 10 weeks (figure 6.8), and the direction of the differences in ignoring is consistent over all ages (Part II fathers ignoring rather less than Part I fathers).

Figure 6.9 shows approaches and leavings by fathers to and from infants. Part II fathers approach infants significantly less often than Part I fathers at 4 and 6 weeks, and again at 18 and 22 weeks, and leave them significantly less often at 4, 6 and 10 weeks, and again at 18 weeks. The effect of the drug on approaching and leaving by fathers is therefore relatively long-lasting.

The results from Part II therefore show that care from fathers who are drugged is not significantly reduced in terms of time spent carrying infants, but is significantly reduced in terms of the number of times fathers pick up infants, the time they spend grooming them, and

Figure 6.3

Mean number of times fathers pick up infants in each Part of the study.
Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.

(No time is spent on fathers from 10 weeks.)

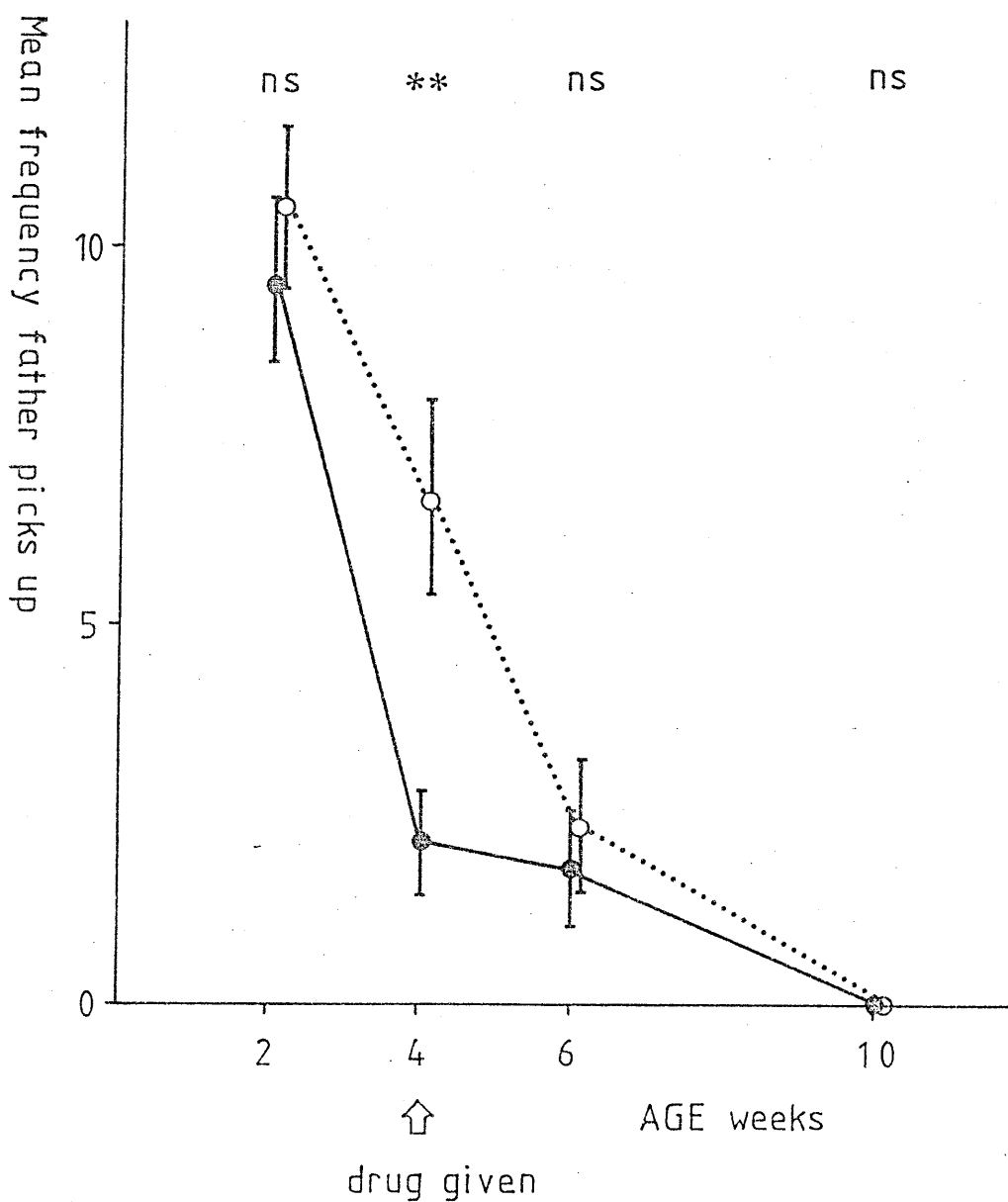


Figure 6.4

Mean percentage of time fathers spend grooming infants in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.

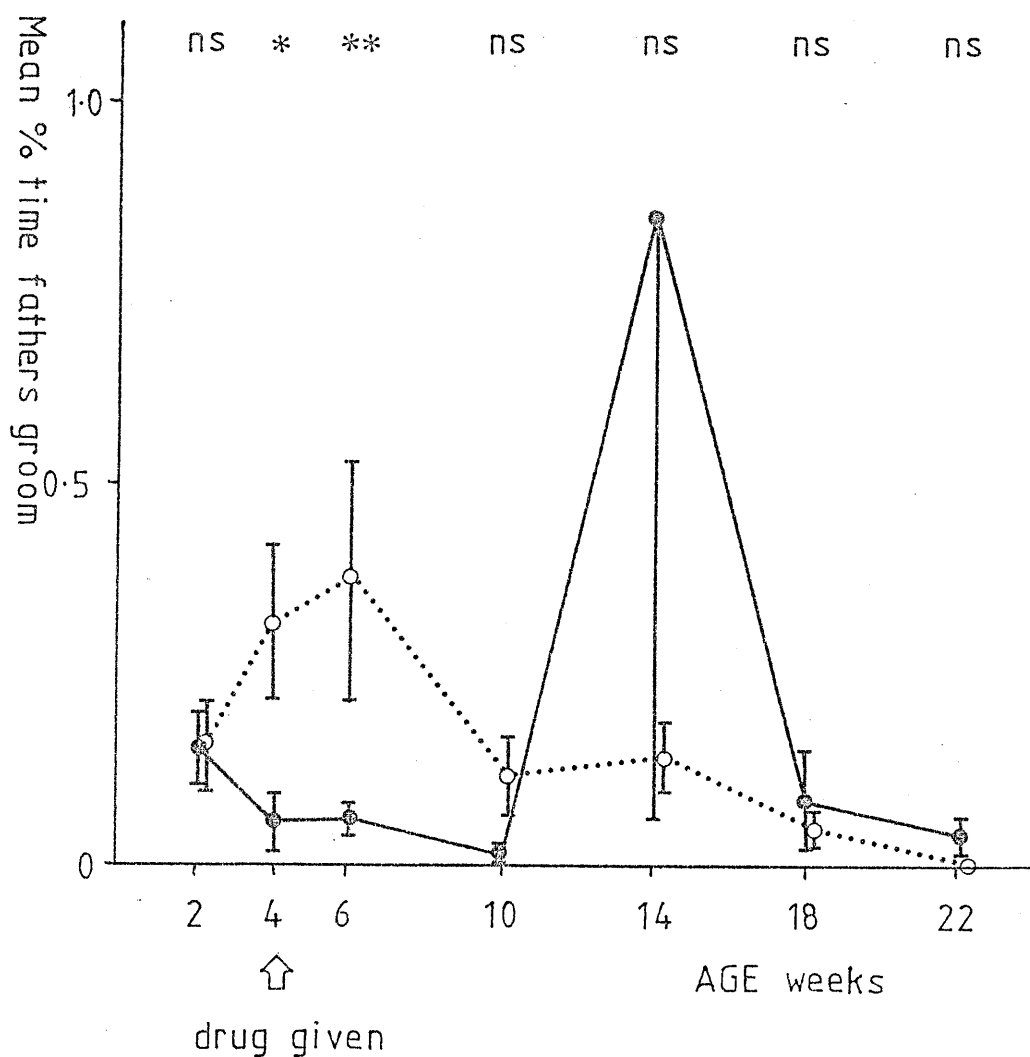


Figure 6.5

Mean percentage of time infants spend in contact with fathers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.

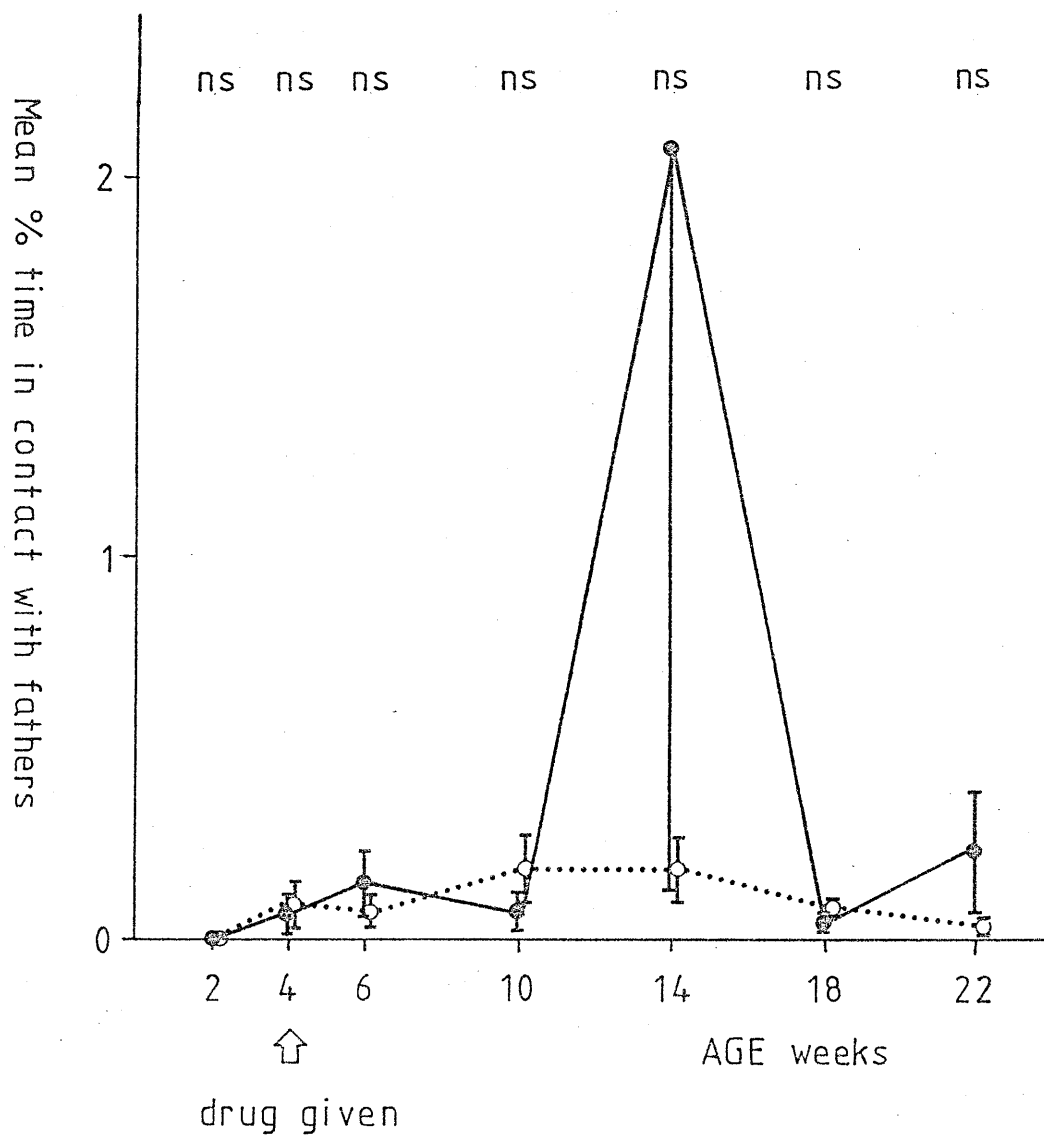


Figure 6.6

Mean number of times fathers ignore infants in each Part of the study.
Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.

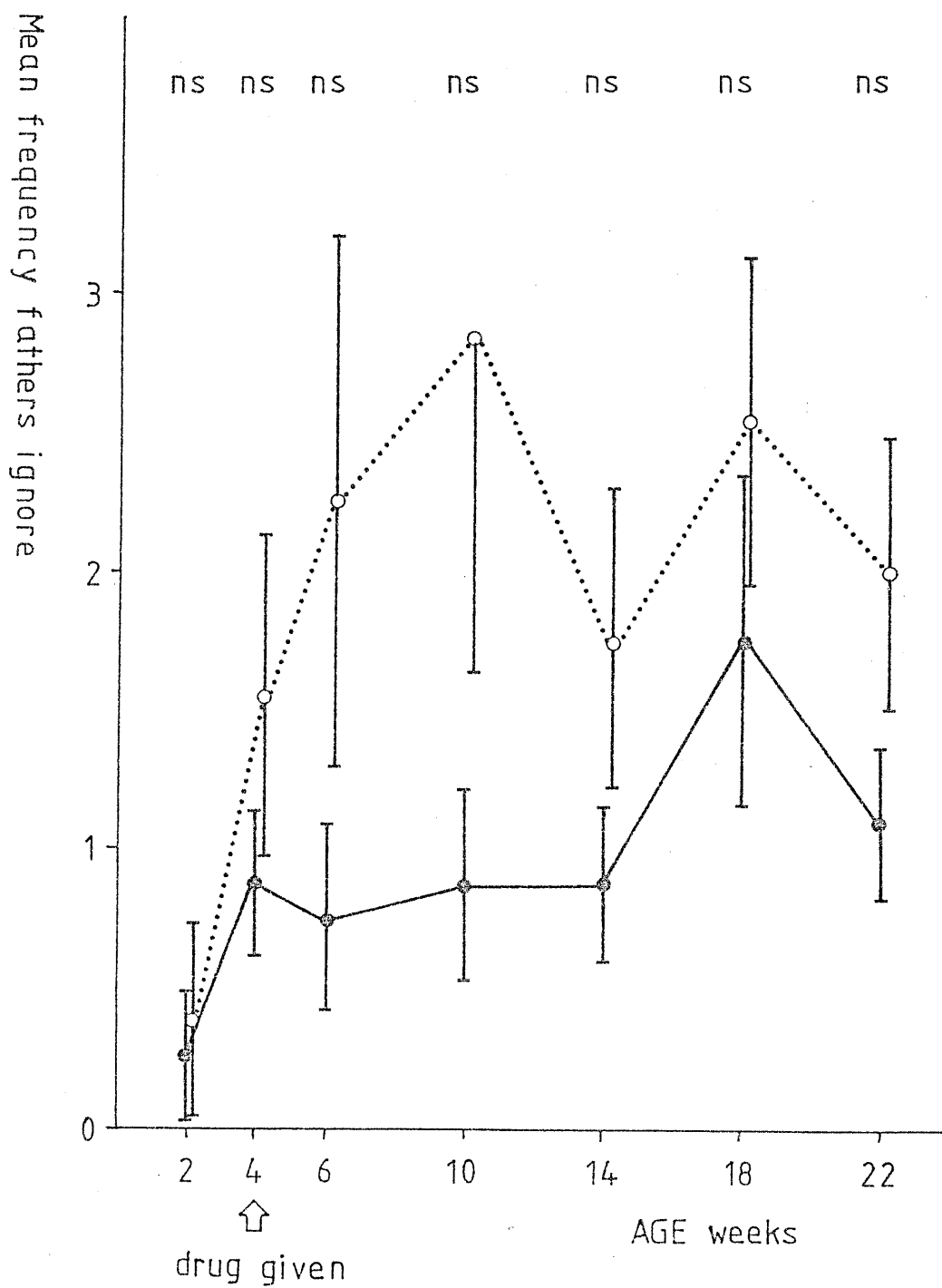


Figure 6.7

Mean frequencies of aggression by fathers towards infants in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.

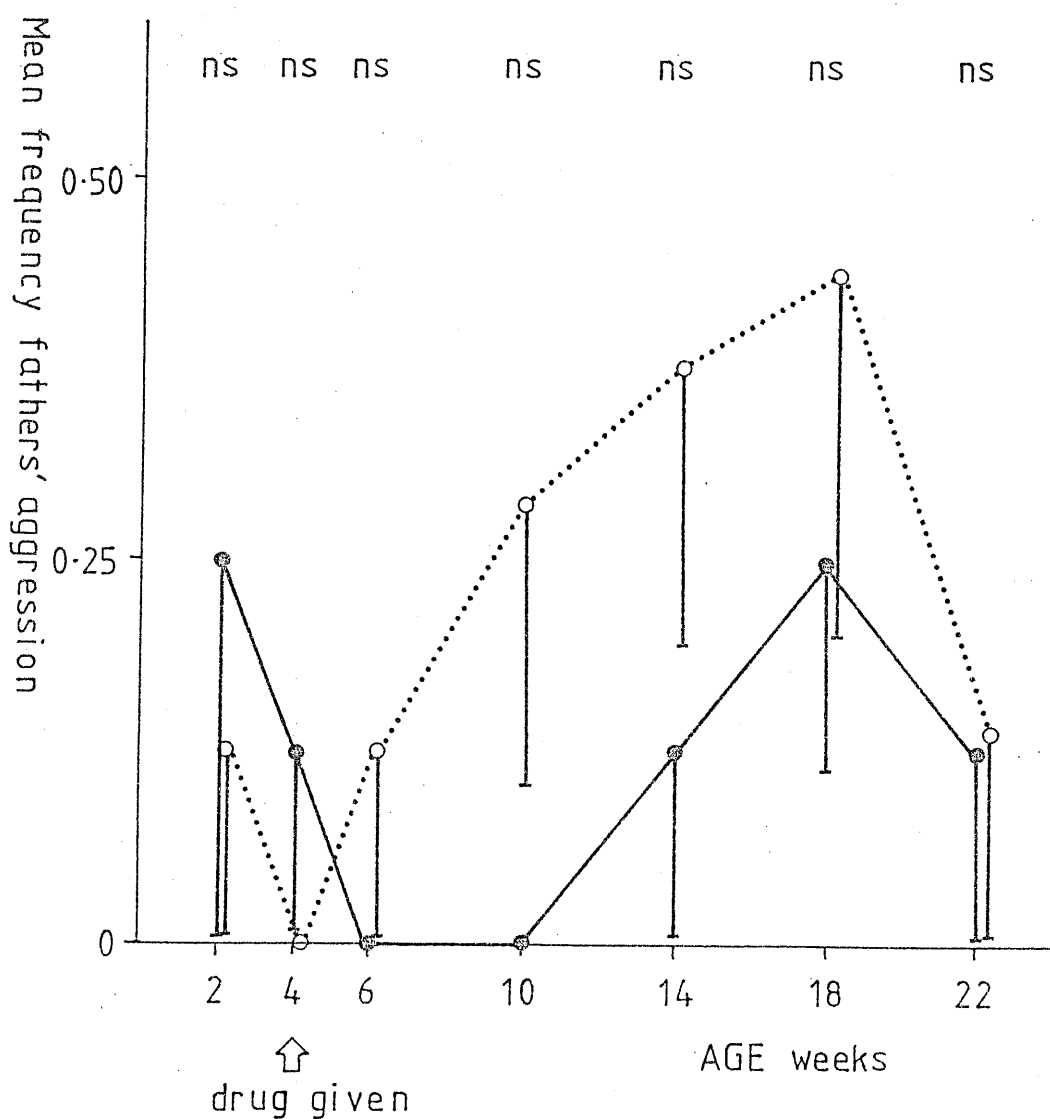


Figure 6.8

Mean absolute frequency of rejections (A.F.R.) and mean relative frequency of rejections (R.F.R.) by fathers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.1.

(No attempts made by Part I infants to get on to fathers at 22 weeks hence no R.F.R. plotted.)

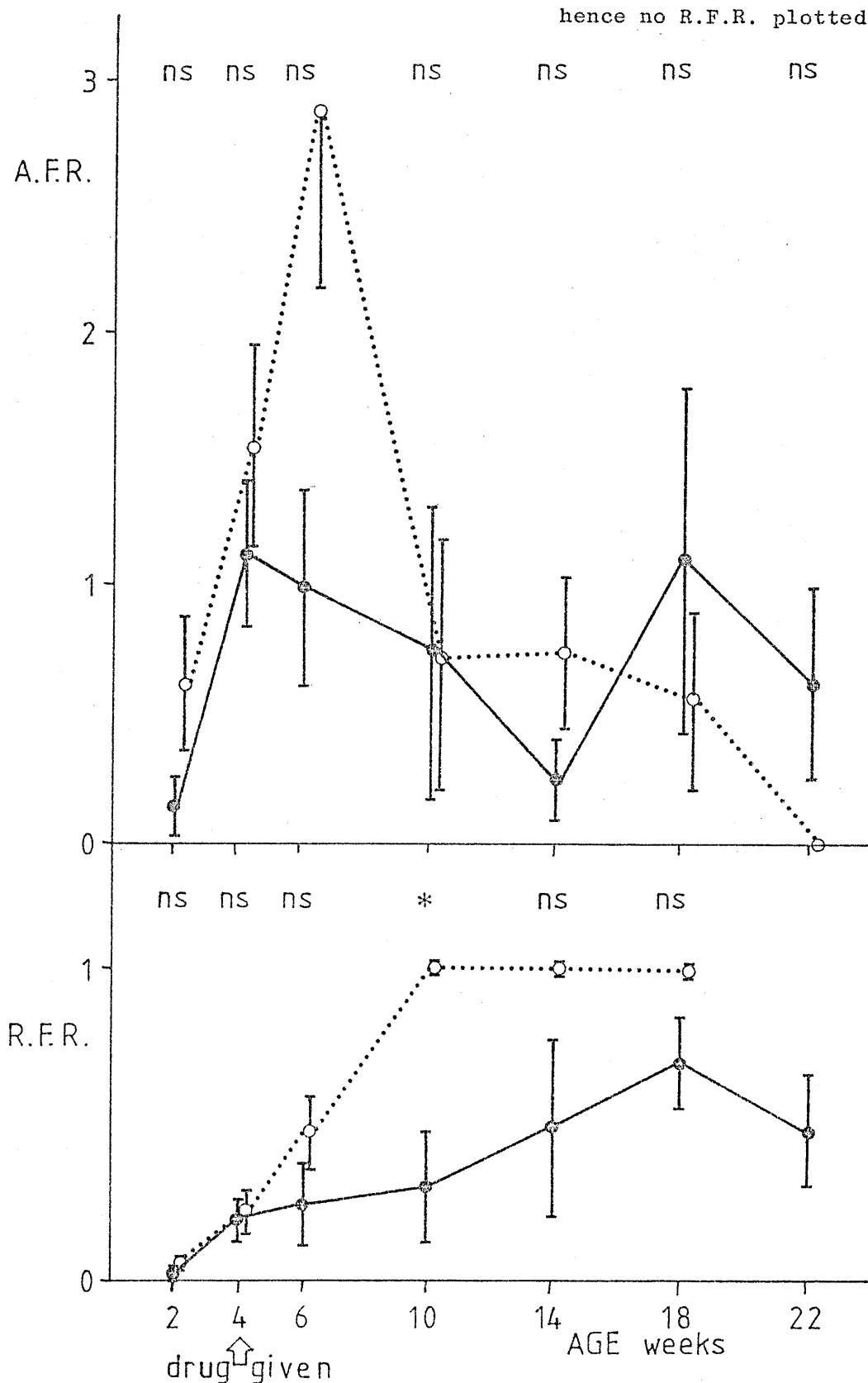
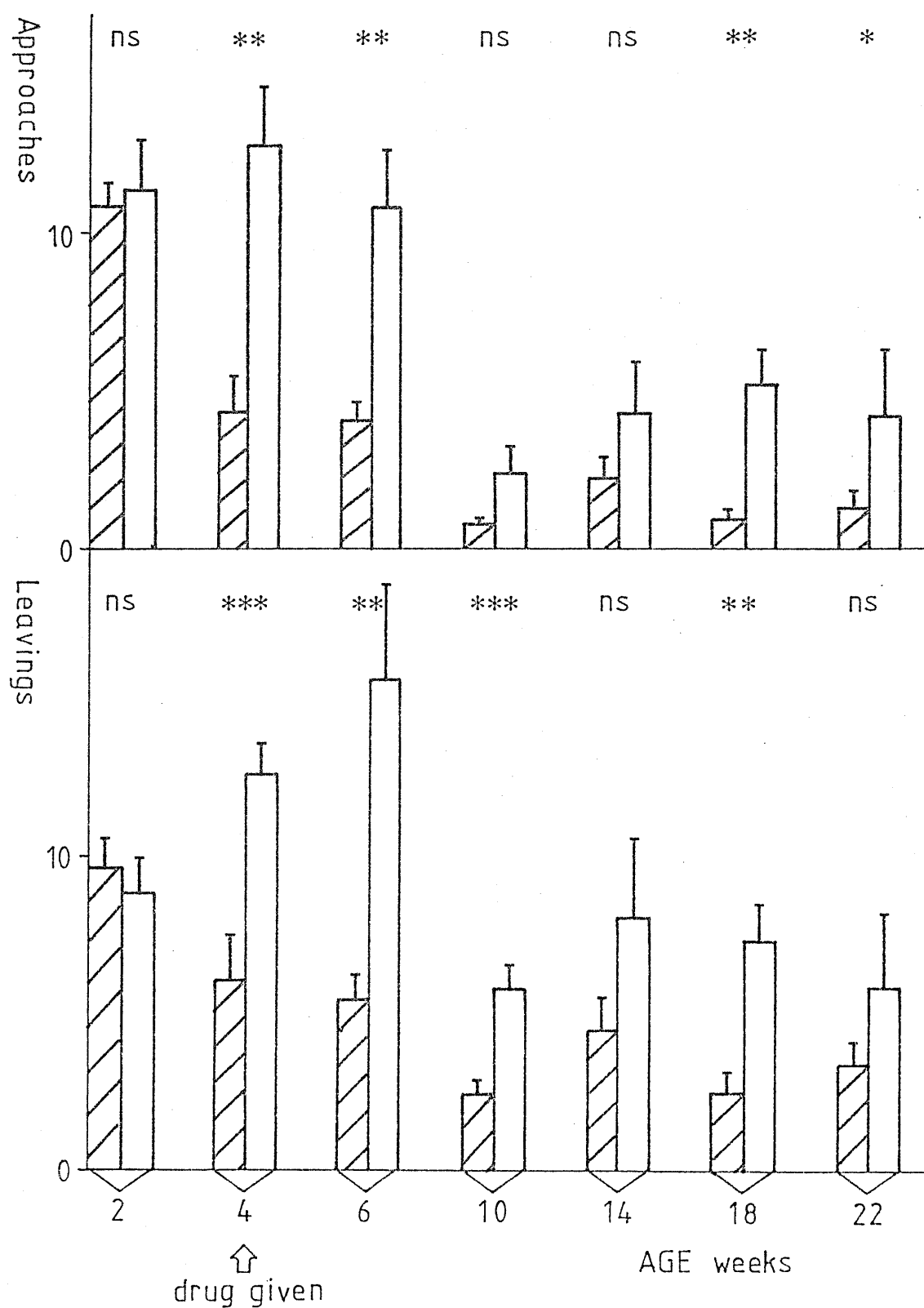


Figure 6.9

Mean frequencies of approaching and leaving by fathers to and from infants in each Part of the study. Vertical lines denote standard errors.

□ Part I infants. ▨ Part II infants.

Conventions as in figure 6.1.



in their overall control of the initiation and termination of interactions as measured by approaching and leaving. These changes are concentrated at the ages of 4 and 6 weeks. However the quality of the care is not significantly altered, in that there is no increase in aggression or in the number of ignores by fathers. The overall effect of the drug on fathers appears to be to make them more 'passive' or 'inert'.

The initial changes in behaviour (at 4 weeks) can tentatively be ascribed to the direct effects of the drug, but where differences continue to 6 or 10 weeks this could be due partly to a reaction of fathers to infants' subsequent responses to their fathers' changed behaviour at 4 weeks.

b) Siblings.

The major contribution of siblings to the infant's social environment from about 10 weeks onwards consists of their acting as play partners (see chapter 4). The effects of the drug on play with siblings will therefore be examined in addition to its effects on caregiving behaviours as defined in section 6.1).

Figures 6.10 to 6.18 compare Part II siblings (drugged when the infants are 14 weeks) with Part I siblings (undrugged controls) in their performance of the following behaviours: Time spent with infant, time spent playing with infant, proportion of time with infant that is spent playing, time in contact with infant, time grooming infant, amount of aggression shown to infant, frequency of ignoring infant, and number of approaches and leavings by siblings to and from infants.

Again it is necessary to bear in mind that any differences in behaviour between Part II and Part I siblings between 4 and 10 weeks may be partly a consequence of the drugging of the infants' fathers at 4 weeks. In general differences between siblings at 14 weeks and after

can be ascribed to the effects of the drug on the siblings since the behavioural changes of the fathers did not last beyond 10 weeks except in the case of approaching and leaving. However, in addition, it is possible that changes in the fathers' or infants' behaviour occurring after the drugging of the fathers may influence siblings' behaviour. Any conclusions therefore must necessarily be tentative.

At 2 weeks of age, i.e. before any drugging had occurred, there are no significant differences between Part I and Part II siblings in any of the behaviours measured except for leaving, Part II siblings leaving infants more often.

Part II siblings spend significantly less time with infants than do Part I siblings at 14 weeks (figure 6.10). This is accounted for by the large and significant drop in the amount of time Part II siblings spend playing with infants (figure 6.11), and is also apparent in the significant reduction in the proportion of their time with infants that is spent in play at this age (figure 6.12). Part II siblings also spend significantly less time playing, and a smaller proportion of time with playing with infants at 6 weeks than Part I siblings. This may be an effect of the drugging of the fathers at 4 weeks (see below).

There are no significant differences between Part I and Part II siblings in the amount of time they spend in contact with infants, or grooming infants, or in the amount of aggression they show towards infants (figures 6.13, 6.14 and 6.15). However since the absolute values of contact grooming and aggression shown by siblings towards infants in Part I are very low, significant reductions in these behaviours would not be expected (compare figures 4.6, 4.4 and 4.49 with the figures for Part II).

Part II siblings ignore infants significantly more often than

Figure 6.10

Mean percentage of time infants spend with their siblings in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Probabilities refer to results of two-tailed Mann-Whitney U tests between data from Part I and Part II at each age.

*** $p < 0.002$. ** $p < 0.02$. * $p < 0.05$. ns non-significant.

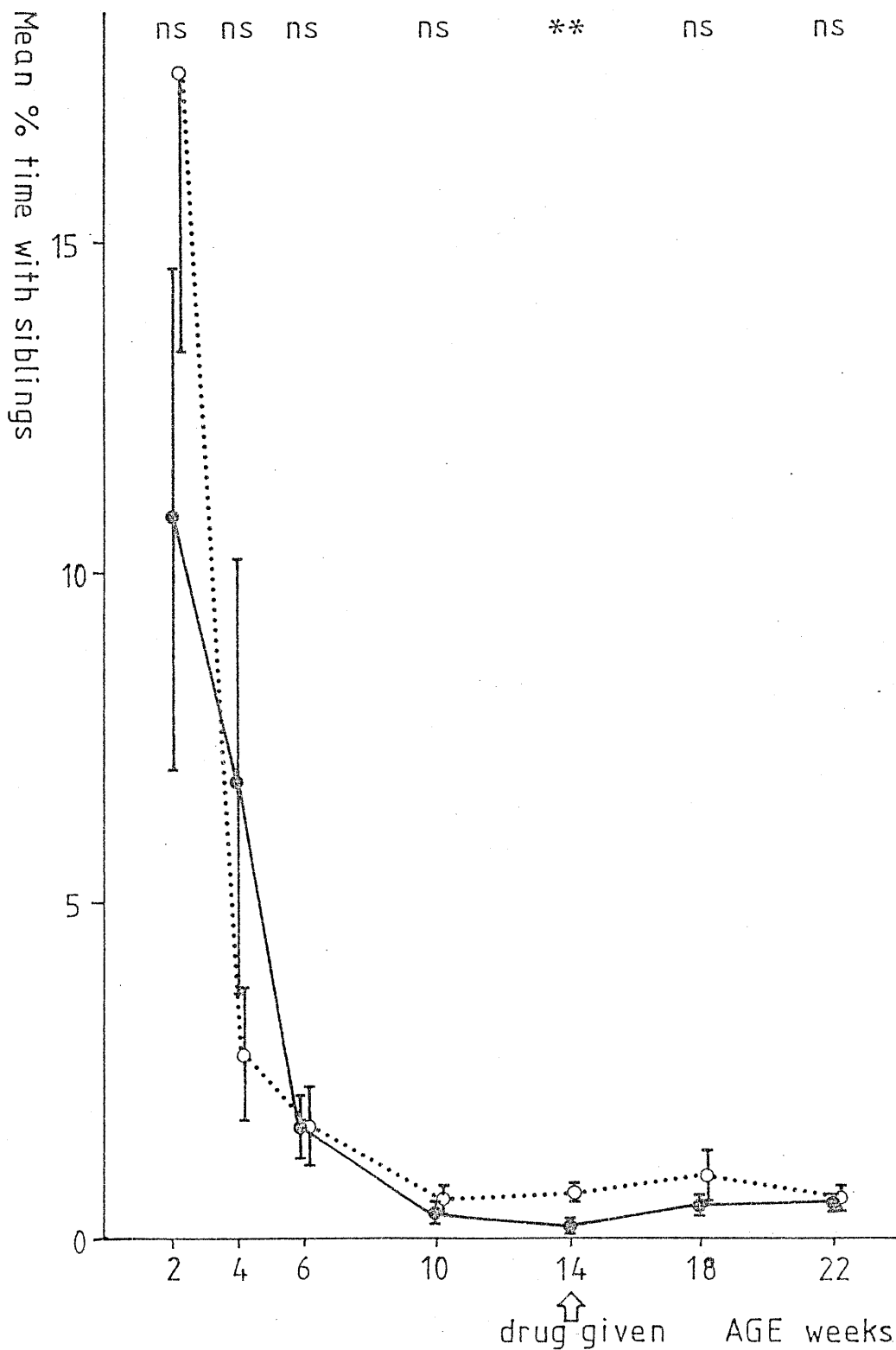


Figure 6.11

Mean percentage of time infants spend playing with their siblings in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.10.

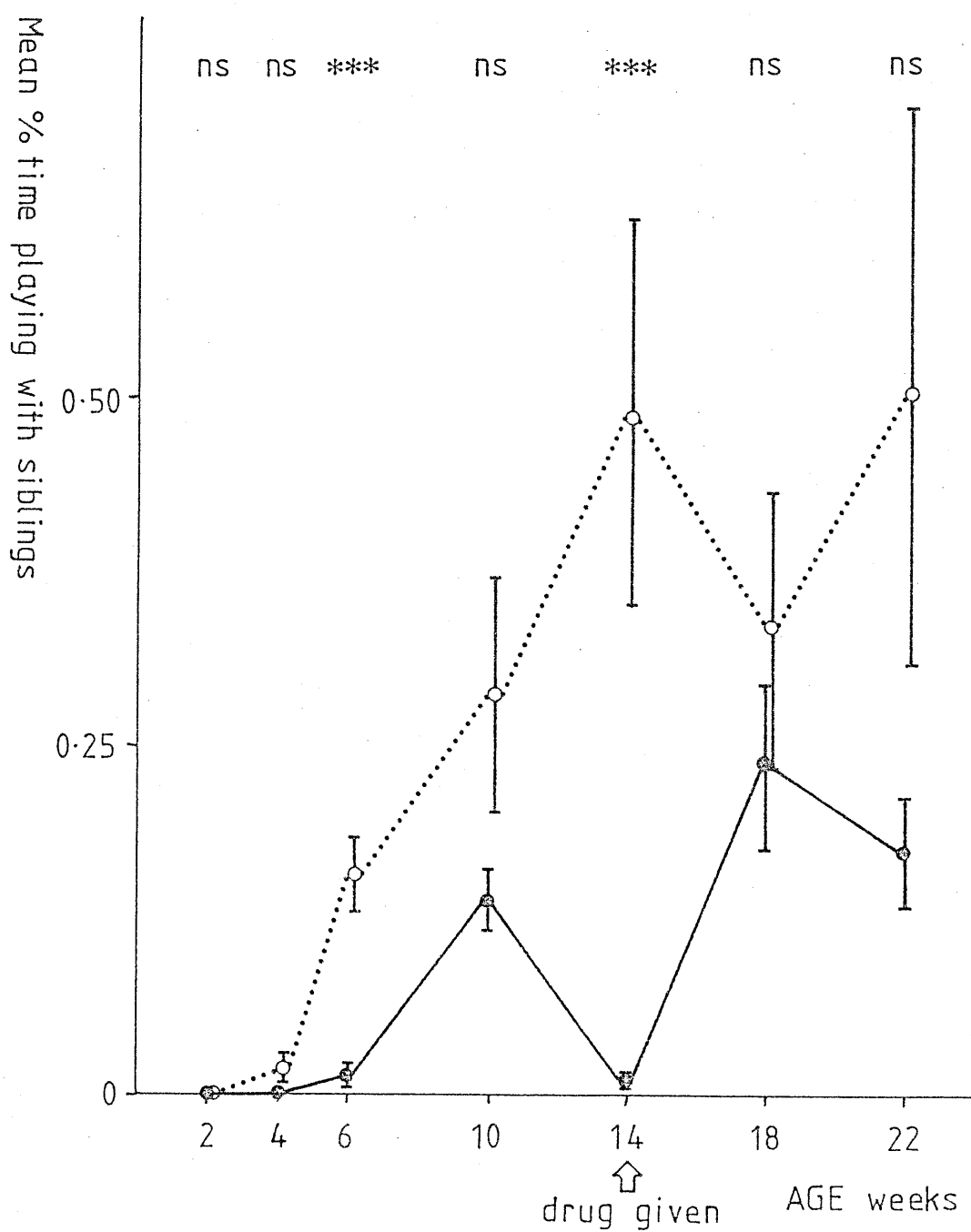


Figure 6.12

Mean proportion of time infants spend with siblings that is devoted to play in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.10.

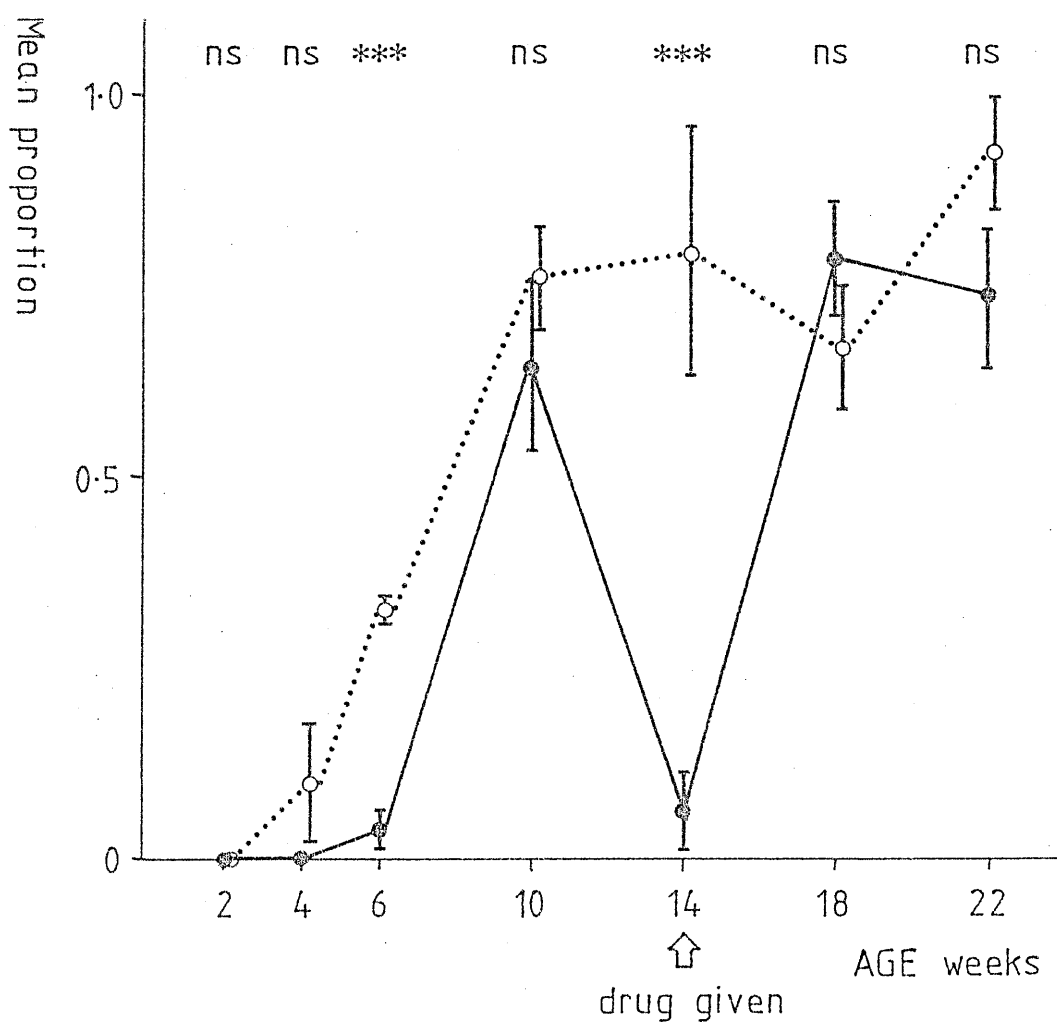


Figure 6.13

Mean percentage of time infants spend in contact with siblings in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.10.

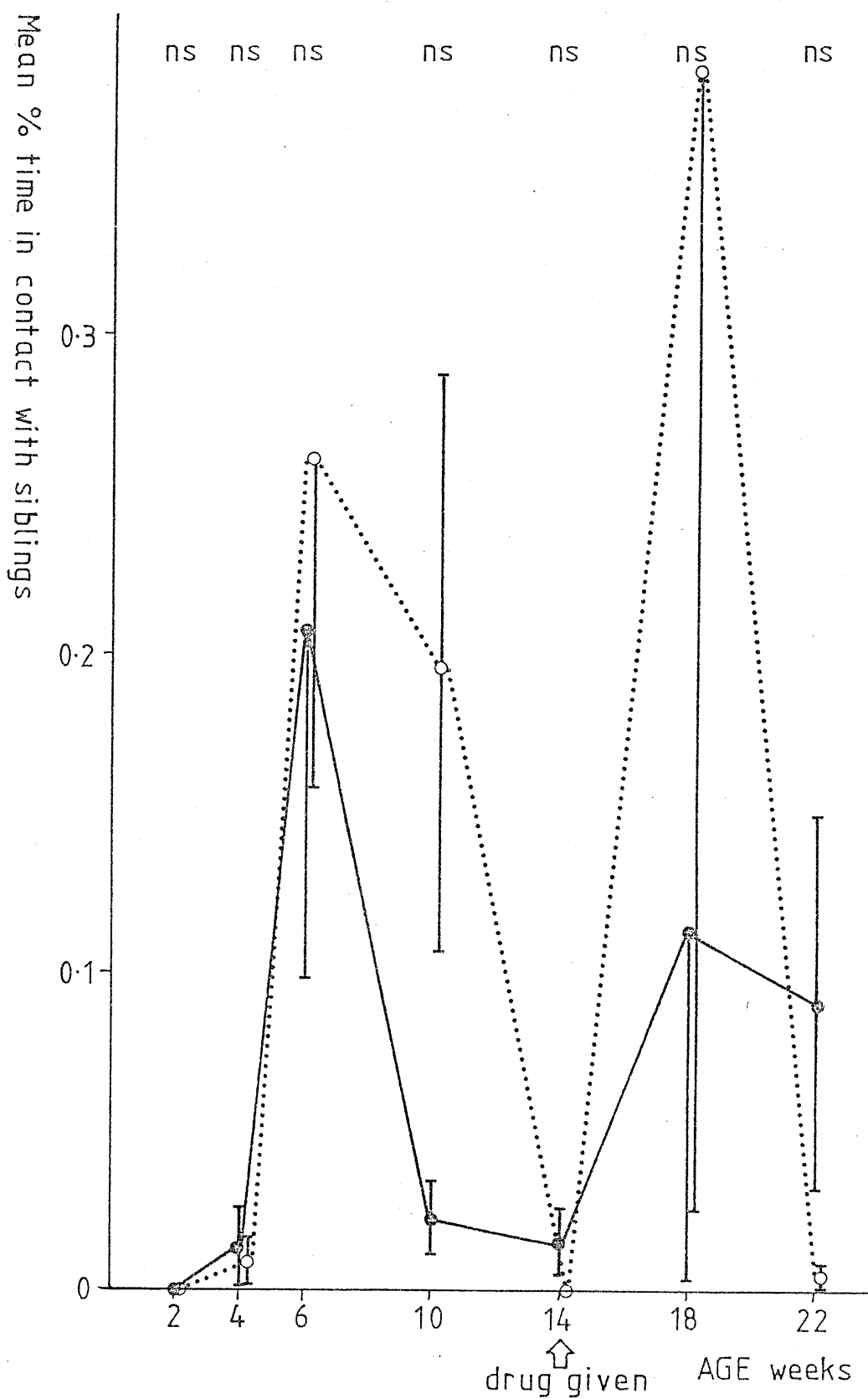


Figure 6.14

Mean percentage of time siblings spend grooming infants in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

@ Data point for Part I infants at 4 weeks has a standard error of 0.25.

This is not shown on the figure due to the large difference in scale compared to the other points. Note split scale on vertical axis.

Other conventions as in figure 6.10.

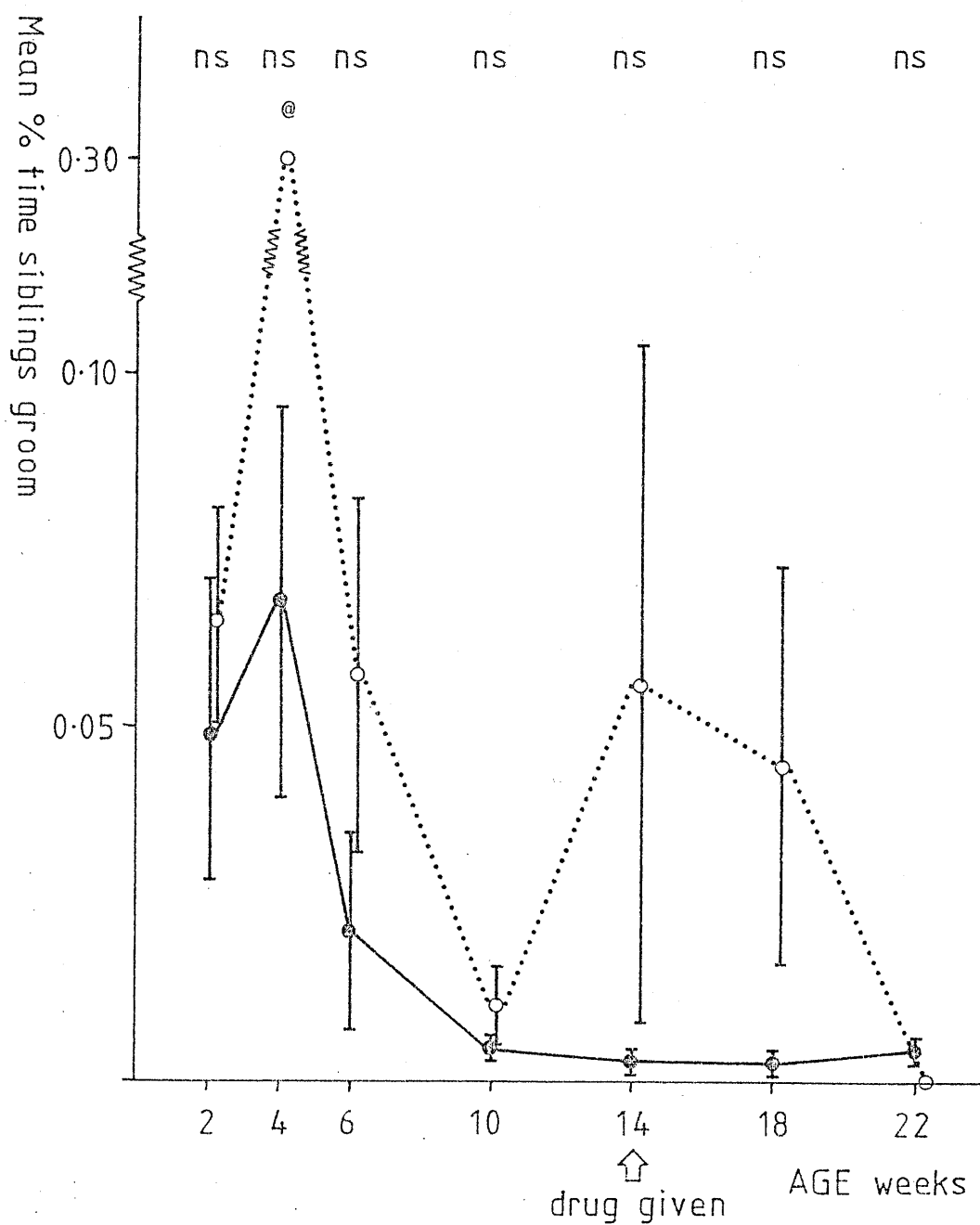
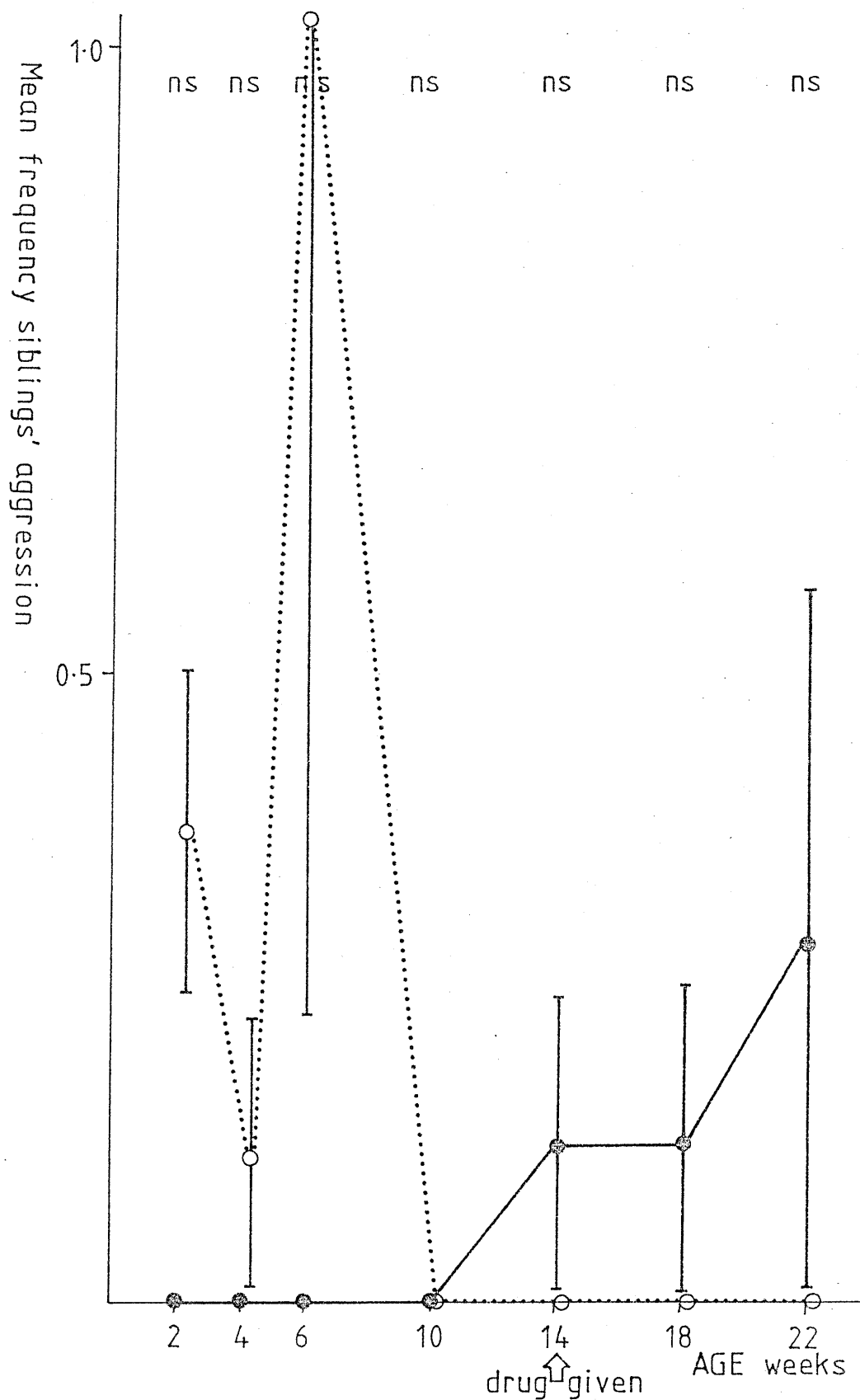


Figure 6.15

Mean frequency of aggression shown by siblings towards infants in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.10.



Part I siblings at 14 weeks of age (figure 6.16). This, together with the reduction in play at this age (figure 6.11) bears out the suggestion made in section 4.5a iii) above that the increase in play by infants with siblings seen in undisturbed conditions around this time is associated with a decrease in ignores from siblings.

The overall decrease in the tendency of Part II siblings (as compared with Part I siblings) to initiate or terminate interactions with infants is reflected in their significantly smaller number of approaches to infants at 2, 6 and 14 weeks, and significantly lower frequency of leavings at 6, 14 and 18 weeks (figures 6.17 and 6.18).

The alteration in the behaviour of siblings which are drugged therefore, is manifest in the form of significantly reduced time with infants and time playing with infants, an increased frequency of ignores and decreased approaching and leaving, all of which occur during the week when the Part II siblings are drugged. Differences in behaviour between Part I and Part II siblings from 4 to 10 weeks, i.e. before siblings are drugged (e.g. less play by Part II siblings at 6 weeks, fewer ignores at 4 weeks, and fewer approaches and leavings at 6 weeks), are possibly an effect of the drugging of the fathers at 4 weeks, either directly as a response by siblings to the father's altered behaviour, or indirectly via changed relationships with other individuals resulting from the effects of the father's altered behaviour on the social nexus. For example, if fathers are made more 'passive' and unresponsive by the drug, they will presumably spend less time grooming mothers. Mothers may therefore try to elicit grooming from siblings, resulting in siblings spending more time interacting with mothers. This would leave siblings less time to interact with infants.

Figure 6.16

Mean number of times siblings ignore infants in each Part of the study.
Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.10.

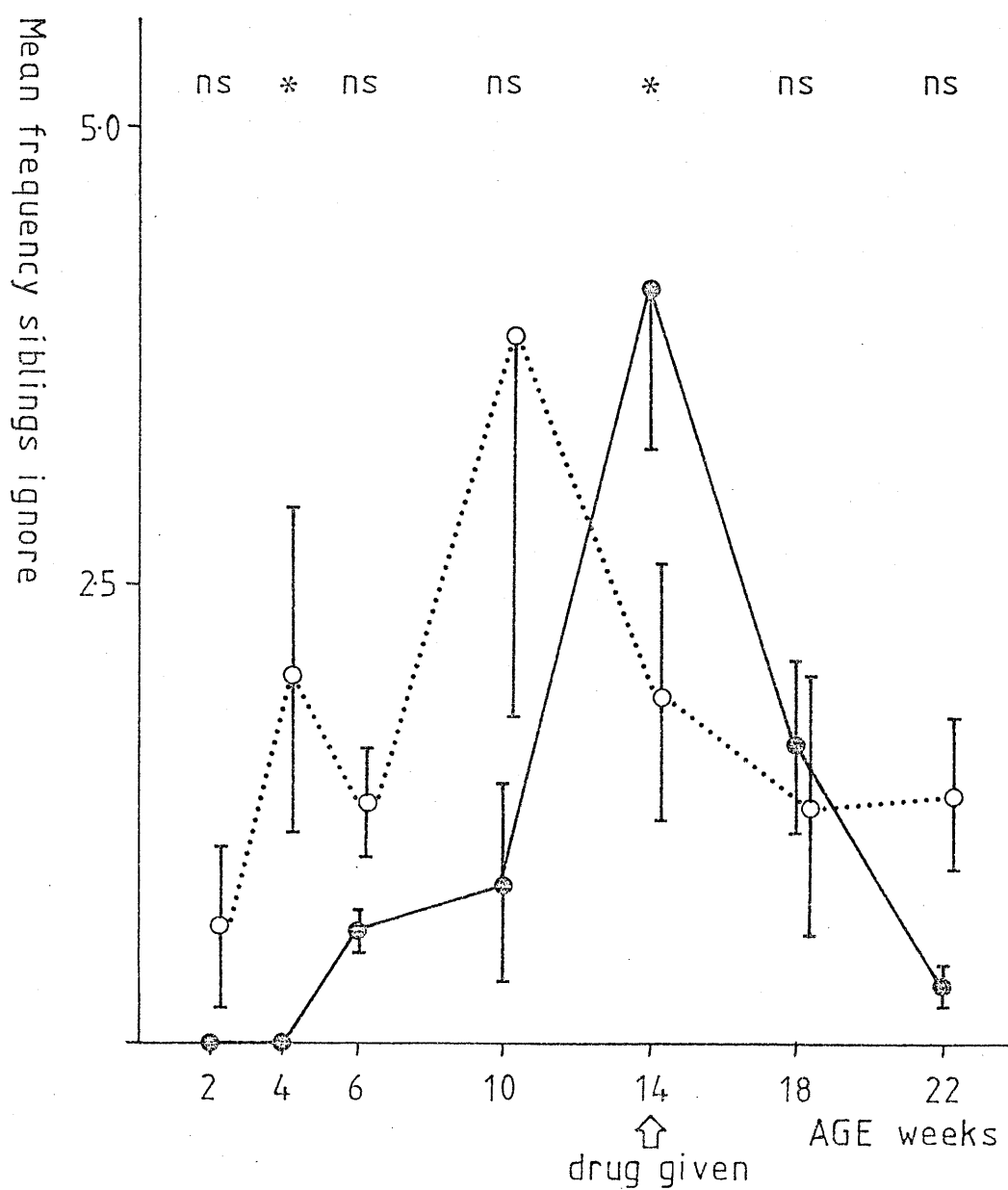


Figure 6.17

Mean frequency of approaches by siblings to infants in each Part of the study. Vertical lines denote standard errors.

Hatched bars denote Part I infants. Open bars denote Part II infants.

Other conventions as in figure 6.10.

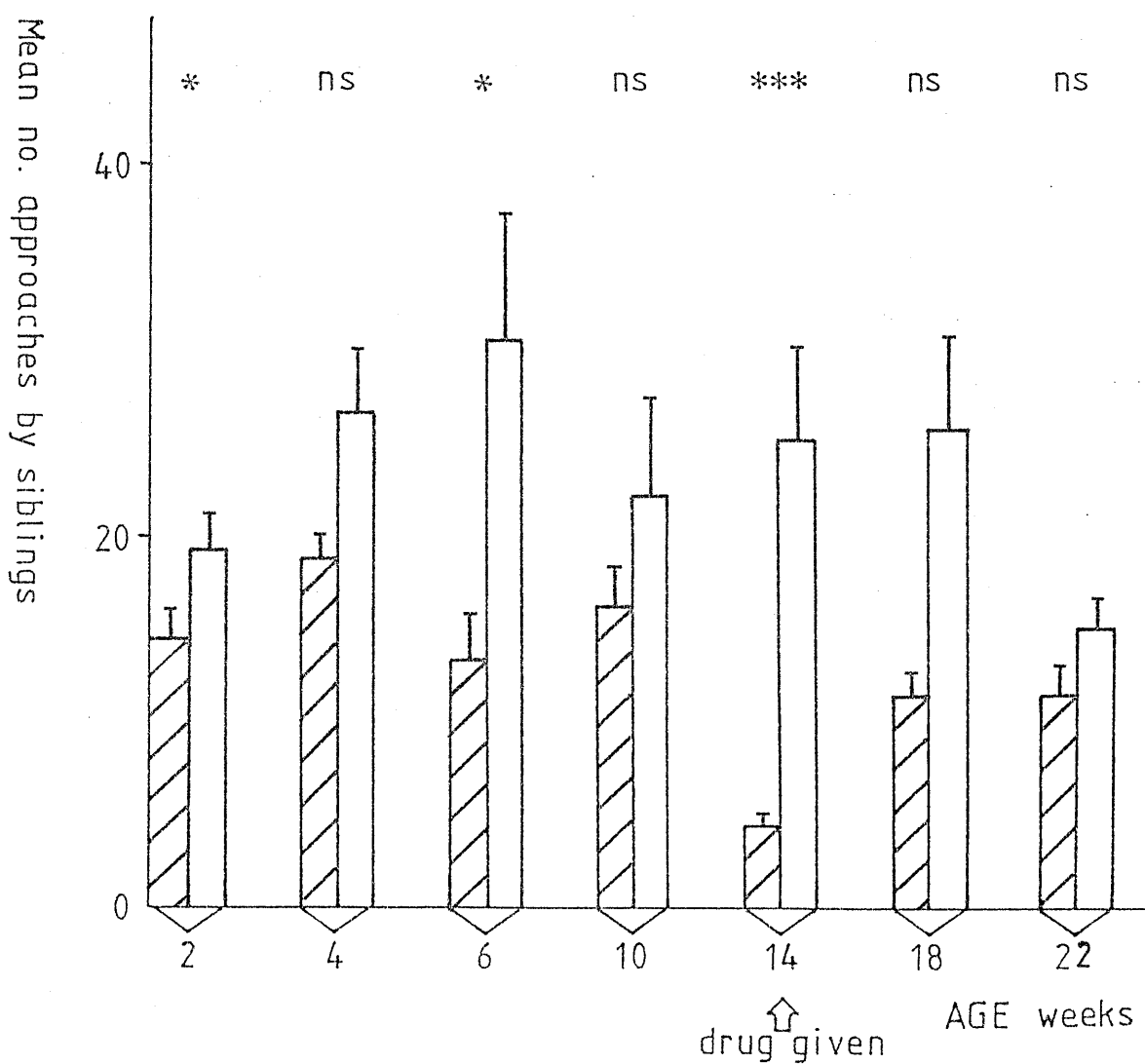
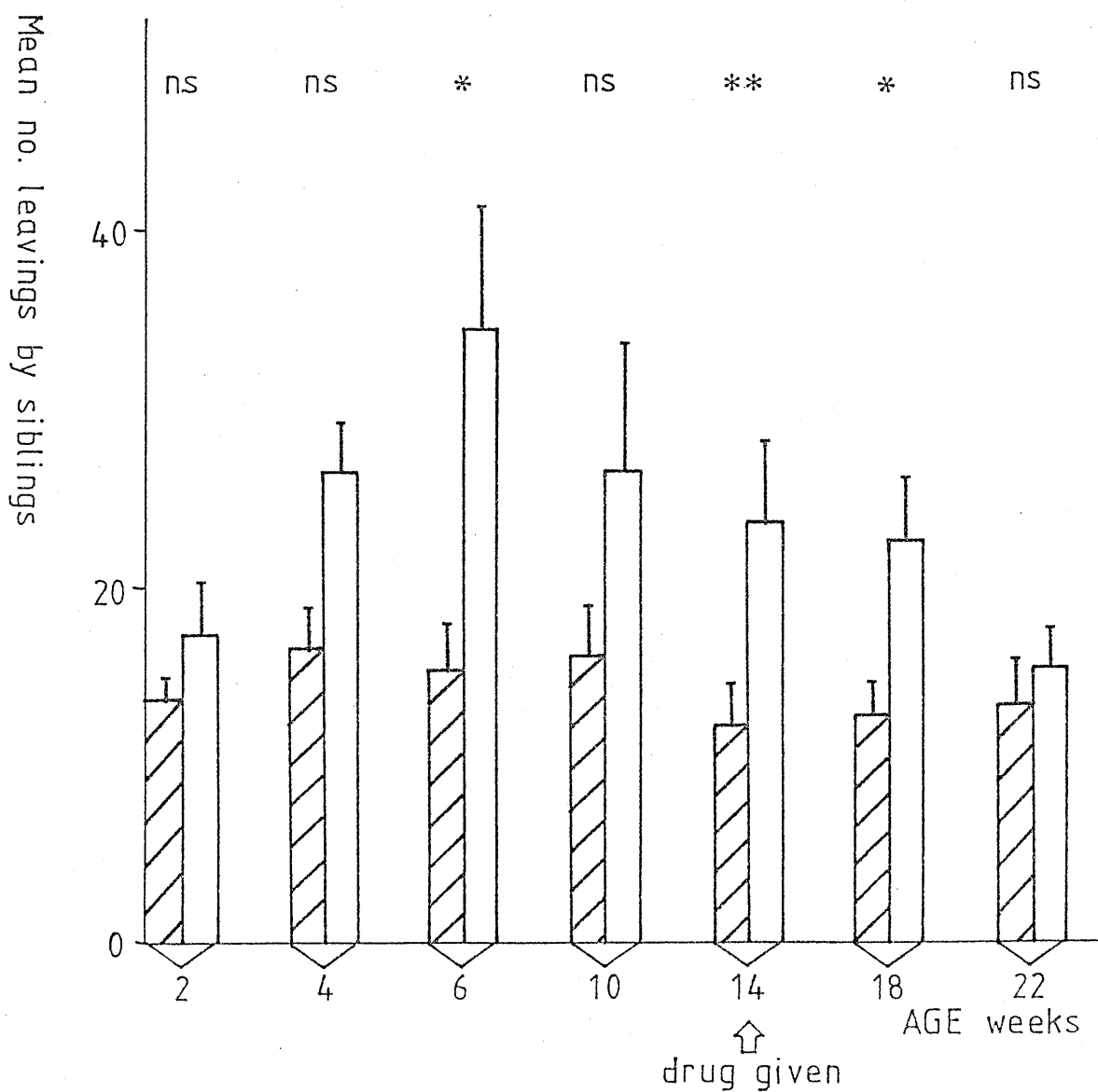


Figure 6.18

Mean frequency of leavings by siblings from infants in each Part of the study. Vertical lines denote standard errors.

Hatched bars denote Part I infants. Open bars denote Part II infants.

Other conventions as in figure 6.10.



6.3) TESTING THE CAREGIVING/CARE-SEEKING HYPOTHESIS

The purpose of this section is to select data to test whether or not the predictions made from the caregiving/care-seeking hypothesis at the end of chapter 4 are borne out when the behaviour of caregivers is altered by drug administration as described in the previous section. The bearing of the results upon the hypothesis is discussed later in section 6.5) and further in chapter 8. The section headings below relate to the chapter 4 predictions.

a) Reducing care will cause the infant to focus on care-seeking activities.

The first prediction stated that if the infant receives less care than usual, its attention will be diverted from non - care-seeking, socializing activities such as play to more direct care-seeking activities. This will be investigated by examining the total amount of play infants from Part II perform at each age, as compared with that performed by Part I infants, together with the total time spent off, the total frequencies of approaching and leaving by infants to and from caregivers, the infants' role in the maintenance of proximity to caregivers, the total amount of huddling, contact and grooming of caregivers, the total frequency of attempts by infants to get on to caregivers, and the total frequency of tantrums given by infants.

No significant differences are found between Part I and Part II infants at 2 weeks of age in any of the above behaviours, though some (play, contact and grooming of caregivers) do not occur at this age.

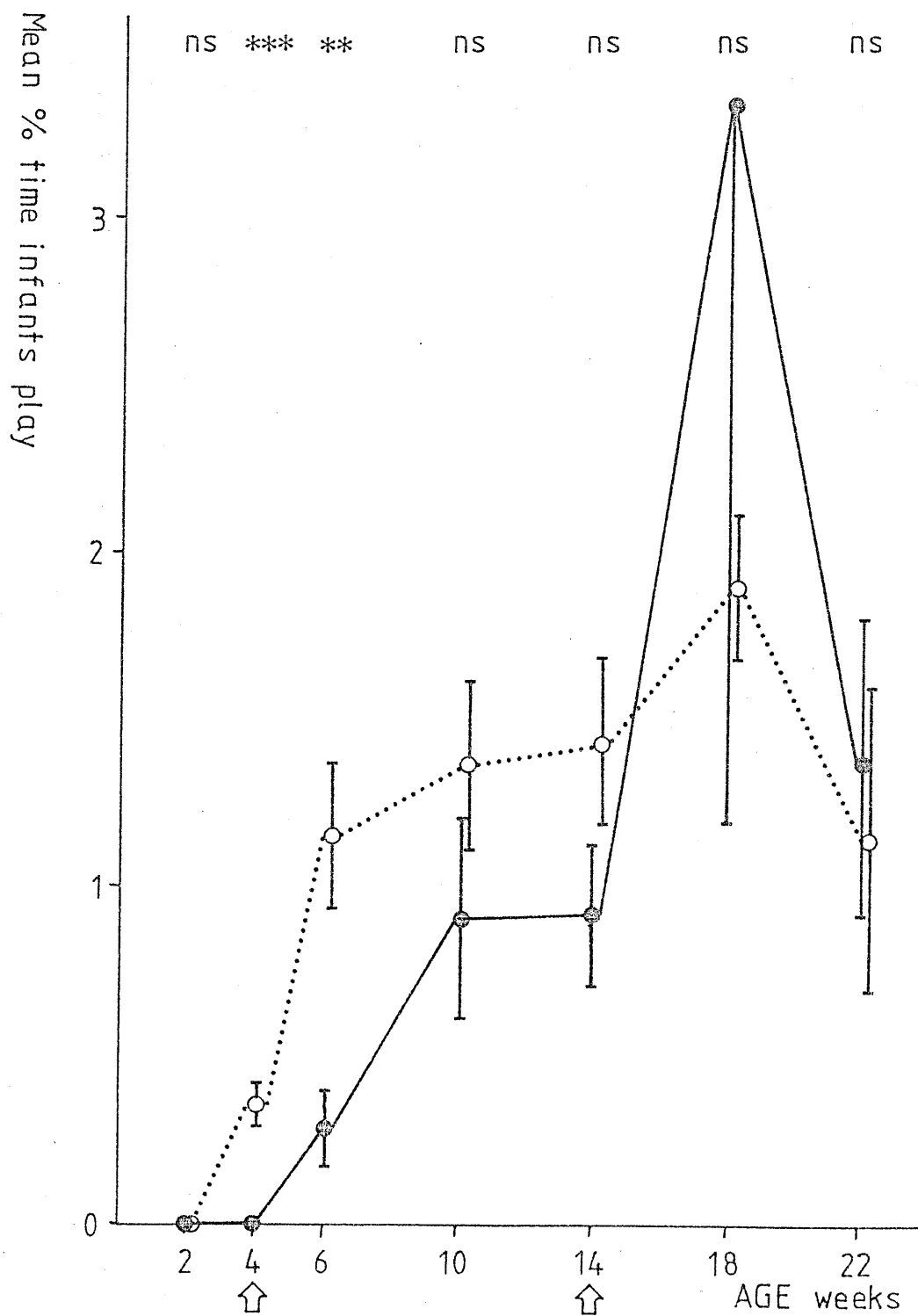
Part II infants spend a highly significantly smaller percentage of time playing than Part I infants at 4 and 6 weeks. They also play less at 10 and 14 weeks though the individual scores at these ages are more variable and these differences are not significant (figure 6.19).

Figure 6.19

Mean total percentage of time infants spend playing in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered. Probabilities refer to results of two-tailed Mann-Whitney U tests between data from Part I and Part II at each age.

*** $p < 0.002$. ** $p < 0.02$. * $p < 0.05$. ns non-significant.



Time off is also significantly reduced in Part II infants at 4 and 6 weeks though not at later ages (figure 6.20). Much of the category 'time off' consists of the infant locomoting and exploring the cage on its own or manipulating objects, i.e. non - care-seeking activities.

These two results indicate that when fathers are drugged at 4 weeks, infants do indeed spend less time engaged in the non - care-seeking activities of play and time off, and this continues to 6 weeks of age (when fathers are still showing less care, see section 6.2a)). However the effect is not significantly noticeable at 14 weeks when the siblings are drugged.

Increased care-seeking by infants could be expected to be revealed in an increase in approaching caregivers (assuming no change in the caregivers tendencies to approach or leave, see section 6.3c)), since this provides the opportunity for contact, grooming, getting on and being picked up, also in an increased role in the maintenance of proximity, increased huddling, contact and grooming of caregivers, more attempts to get on, and more tantrums (since tantrums would call attention to the infant's requirement for care). More time on is not necessarily expected since the Part I results showed that time on is primarily controlled by caregivers rather than by infants (see chapter 4). Not all of these predictions are borne out.

Approaching and leaving decrease rather than increase in Part II over Part I infants, and this is highly significant at 6 and 14 weeks (figures 6.21 and 6.22). Part II infants show a significant increase in the relative role they play in maintaining proximity to caregivers at 14 weeks (figure, 6.23), but this is not the case at earlier ages.

Part II infants spend significantly more time huddling than Part I infants at 4 weeks (figure 6.24), and rather more time in

Figure 6.20

Mean percentage of time infants spend off in each Part of the study.
Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered.
Conventions as in figure 6.19.

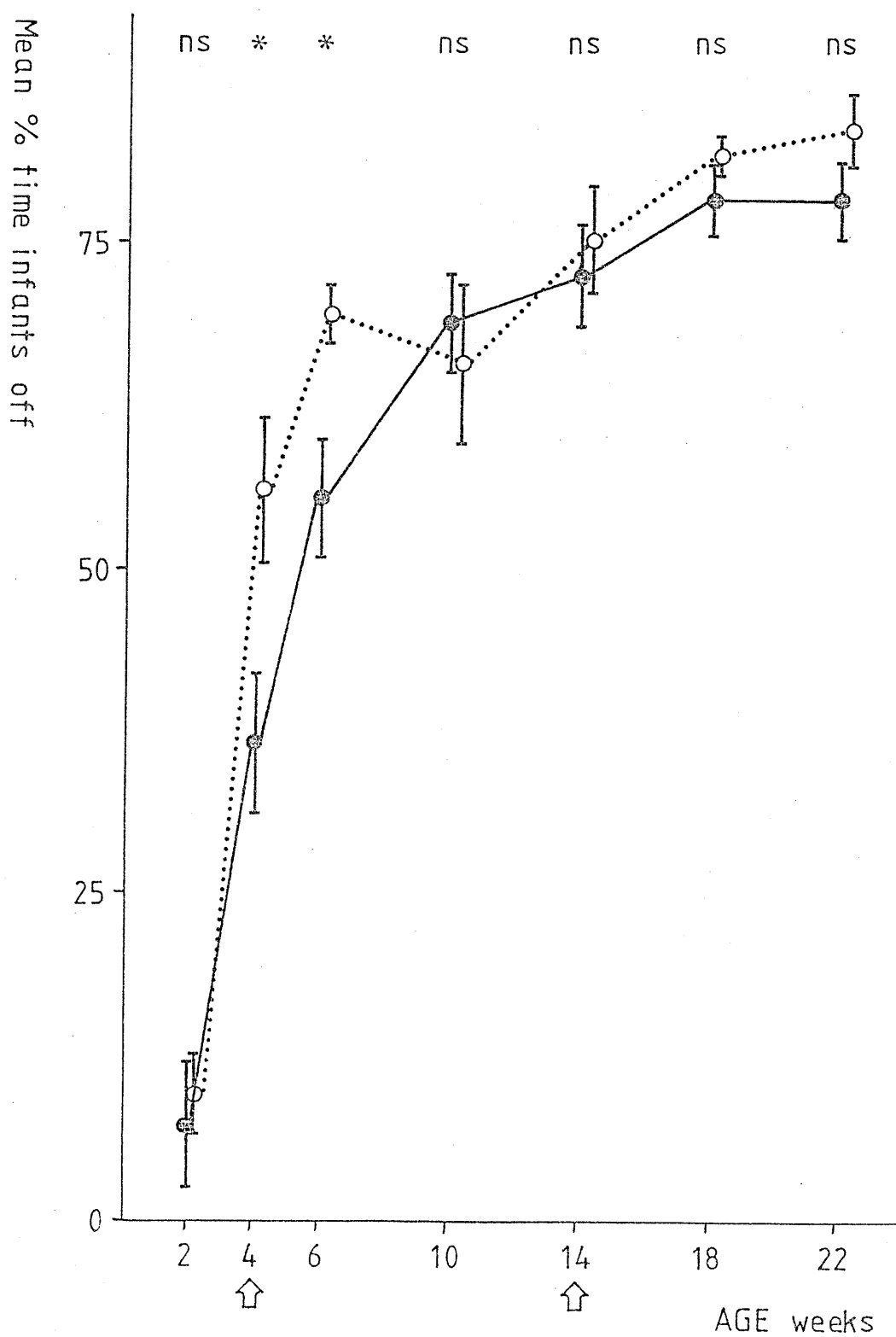


Figure 6.21

Mean frequencies of approaches made by infants to all caregivers in each Part of the study. Vertical lines denote standard errors.

□ Part I infants. ▨ Part II infants. ⇨ drug administered. Conventions as in figure 6.19.

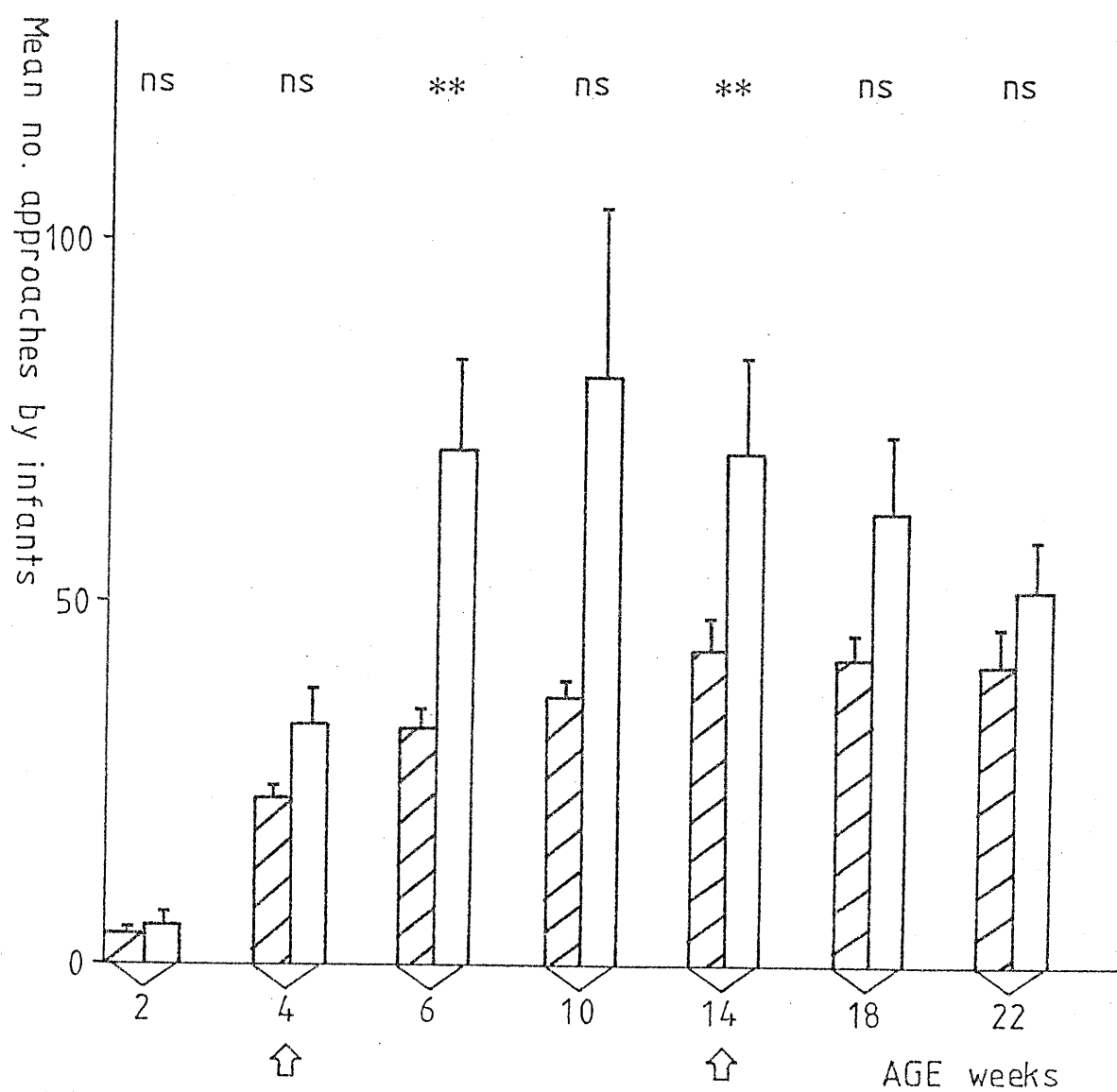


Figure 6.22

Mean frequencies of leavings made by infants from all caregivers in each Part of the study. Vertical lines denote standard errors.

□ Part I infants. ▨ Part II infants. ⇨ drug administered. Conventions as in figure 6.19.

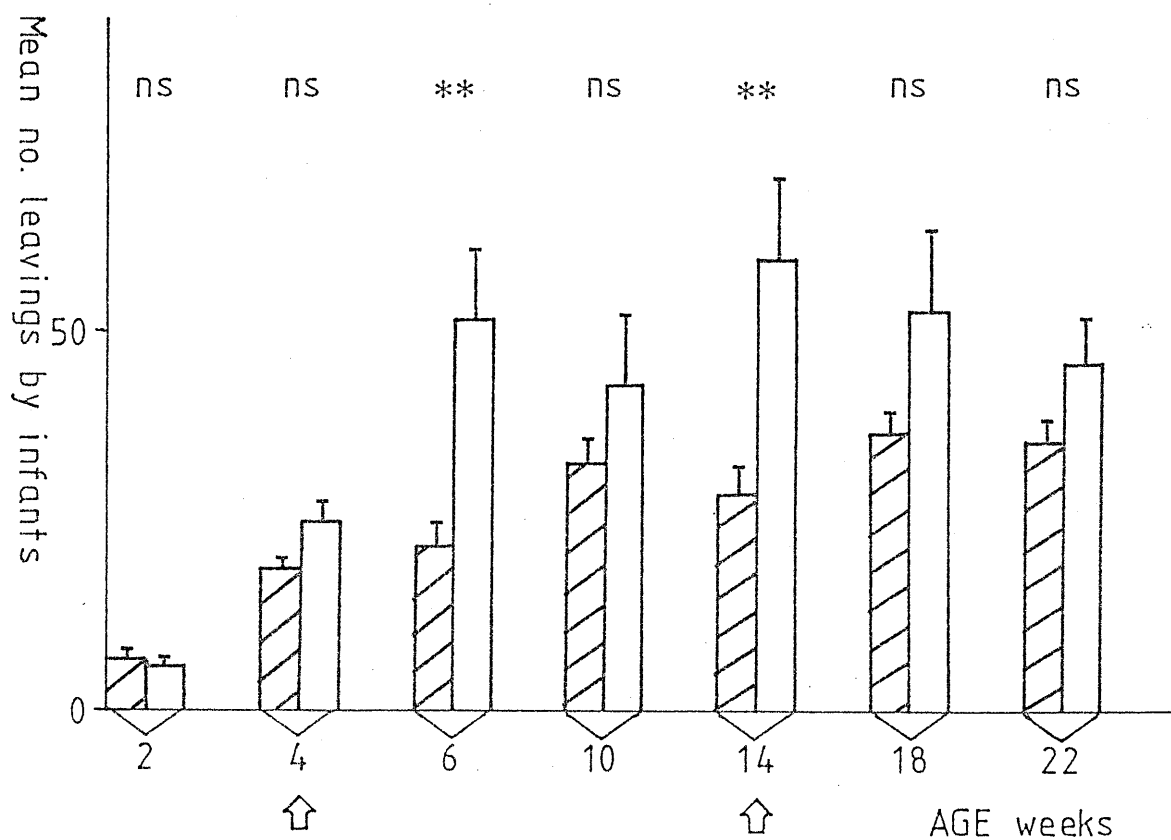


Figure 6.23

Maintenance of proximity to caregivers by infants in each Part of the study: Mean percentage of all approaches between caregivers and infants that are due to infants minus mean percentage of all leavings that are due to infants. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered. Conventions as in figure 6. 19.

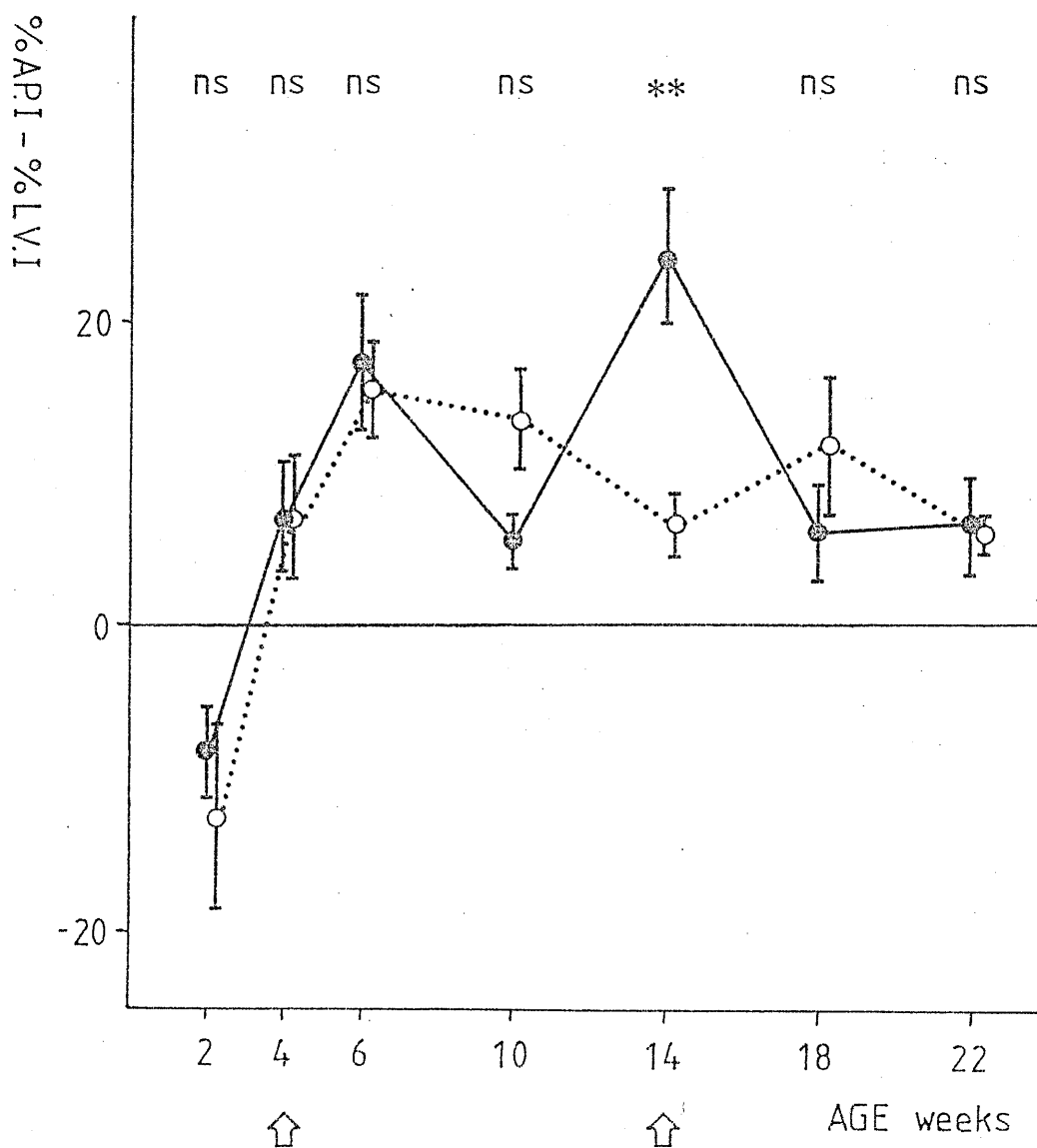
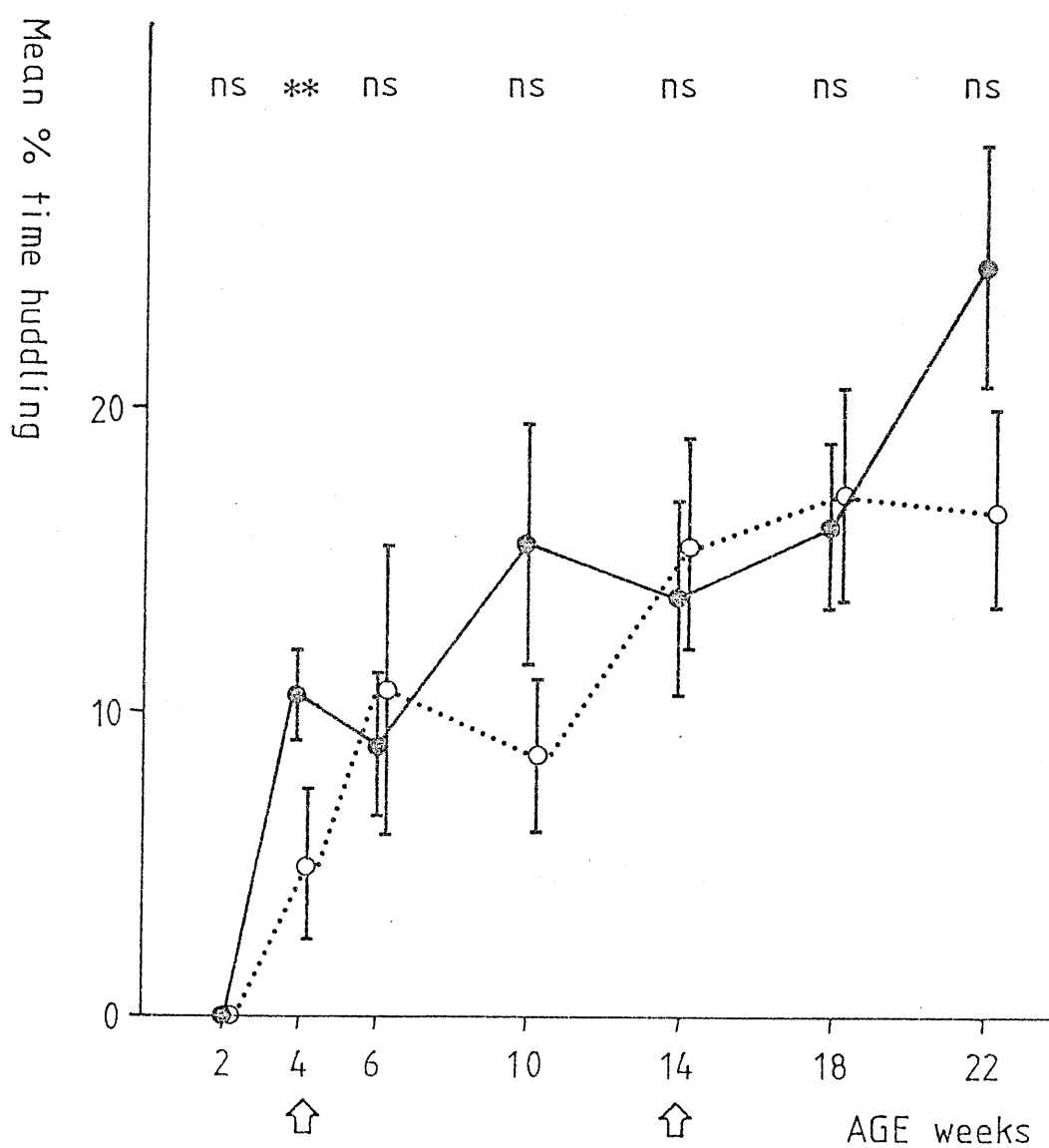


Figure 6.24

Mean percentage of time infants spend in family huddles in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered. Conventions as in figure 6.19.



contact with caregivers at 4 and 6 weeks though this is not significant (figure 6.25). Huddling is not defined as care from the caregivers' point of view (see section 6.1)) since it requires no action by the caregivers who are themselves already huddling. However, from the infant's point of view, joining a family huddle can be seen as a technique to gain contact with one or several caregivers and hence as a form of care-seeking. Part II infants also show less grooming of caregivers than do Part I infants, the differences being significant at 6 weeks and highly significant at 10 weeks (figure 6.26).

In contrast, Part II infants make fewer attempts to get on to caregivers, and this is highly significant at 6 weeks (figure 6.27). Some of these attempts are directed at twins in Part II (figure 6.35), though this was never seen to occur in Part I (section 4.3b)). There are no significant differences at any age between Parts I and II infant in their total frequency of tantrums (figure 6.28). Differences might have been expected if infants use tantrums as a means of soliciting care. However if infants simply throw tantrums to express discomfort of some kind, it is interesting to note that in this case Part II infants are no more uncomfortable than Part I infants despite the reduced care they are receiving from fathers at 4 and 6 weeks, and despite the reduced amount of social interactions with siblings at 14 weeks.

The decrease in care from fathers at 4 and 6 weeks seems to have more effect (i.e. more infant behaviours are altered) than the decrease in interactions with siblings at 14 weeks.

Overall, reduced levels of care and social interaction are associated with a decrease in approaching and leaving, a decrease in grooming and a decrease in the number of attempts to get on to caregivers. Play and time off are also decreased at 4 and 6 weeks. Care is sought in the early weeks through increased huddling with caregivers, and social

Figure 6.25

Mean total percentage of time infants spend in contact with caregivers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered. Conventions as in figure 6.19.

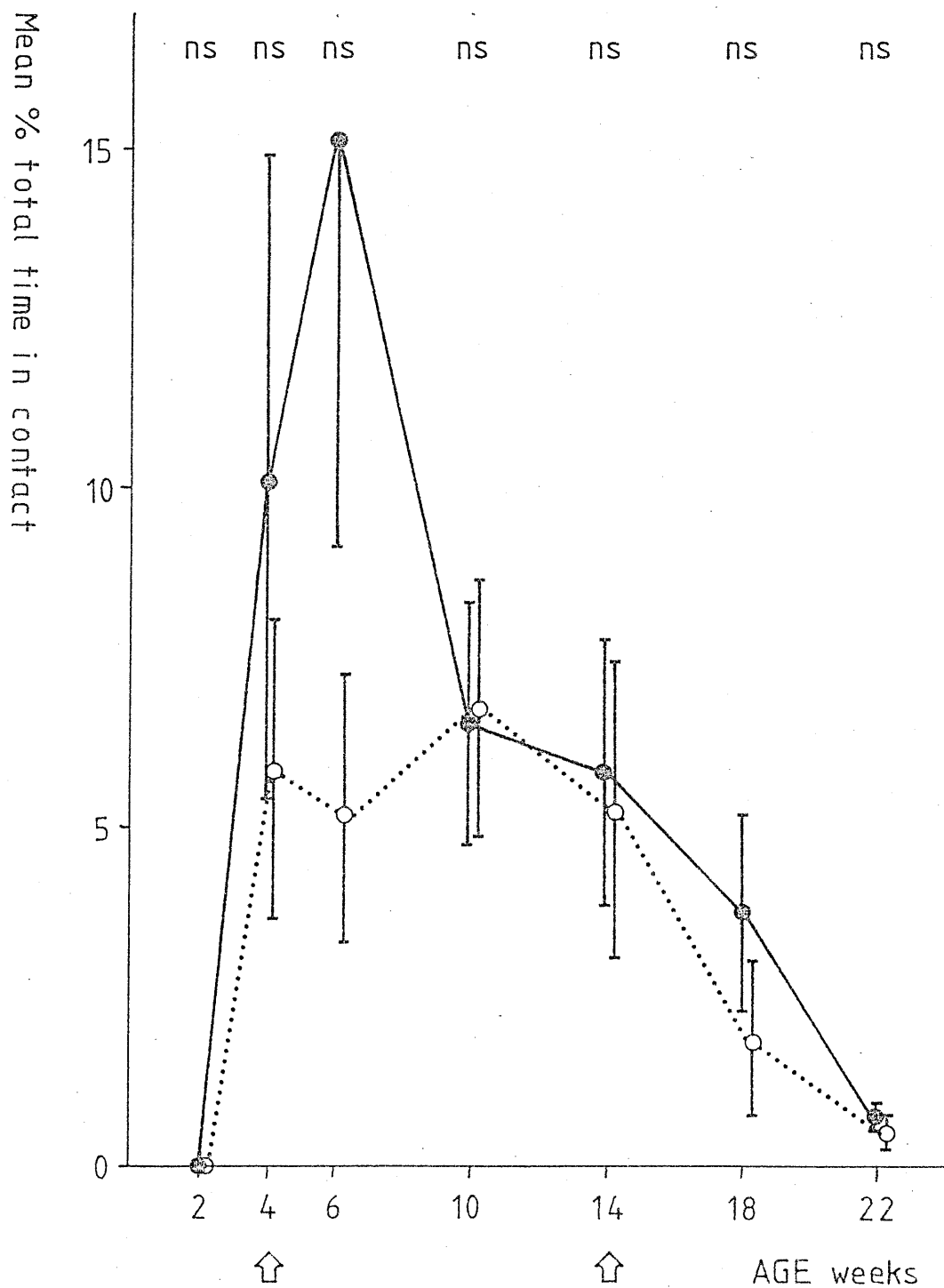


Figure 6.26

Mean percentage of time infants spend grooming caregivers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered. Conventions as in figure 6.19.

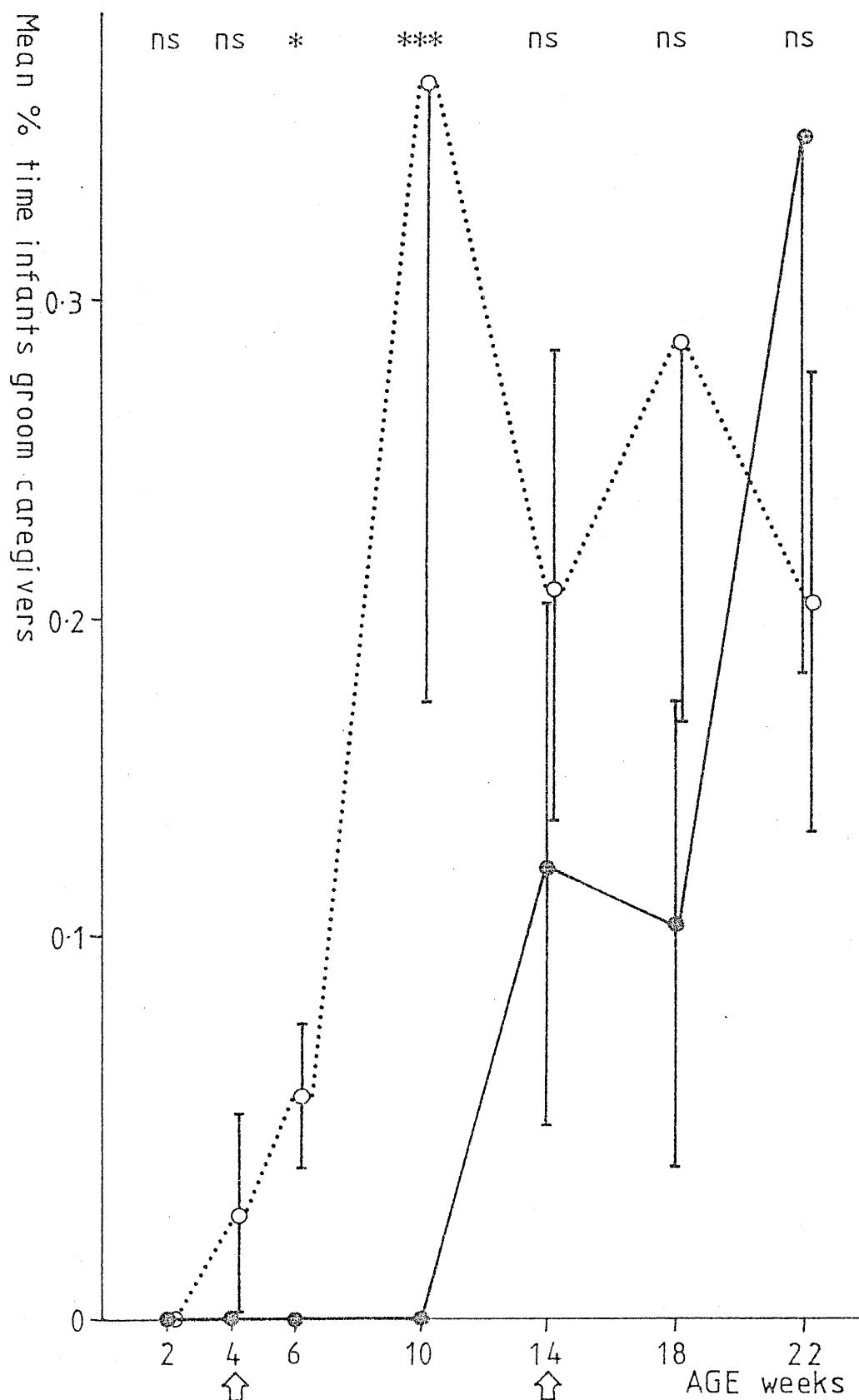


Figure 6.27

Mean total frequencies of attempts by infants to get on to parents and siblings in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered. Conventions as in figure 6.19.

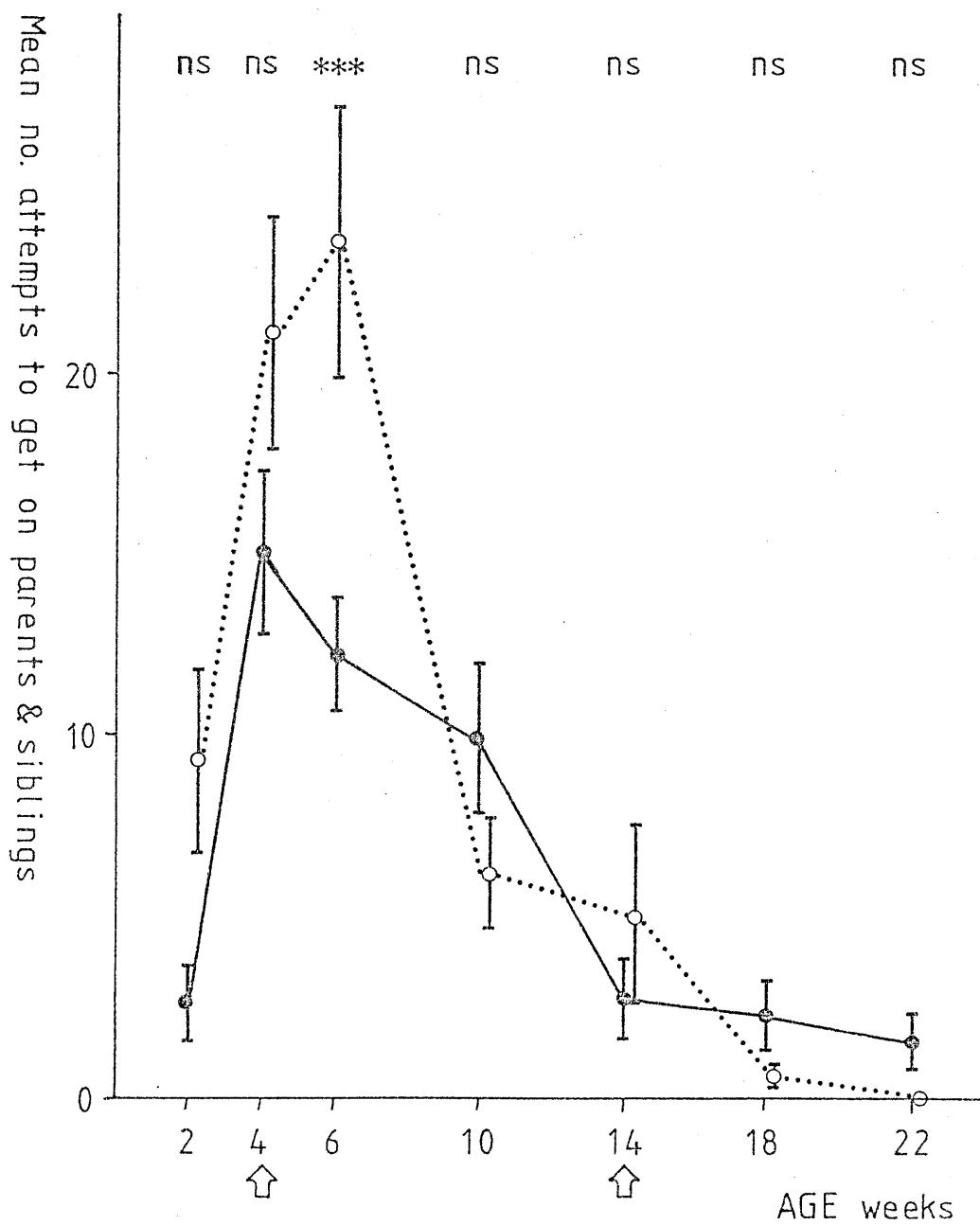
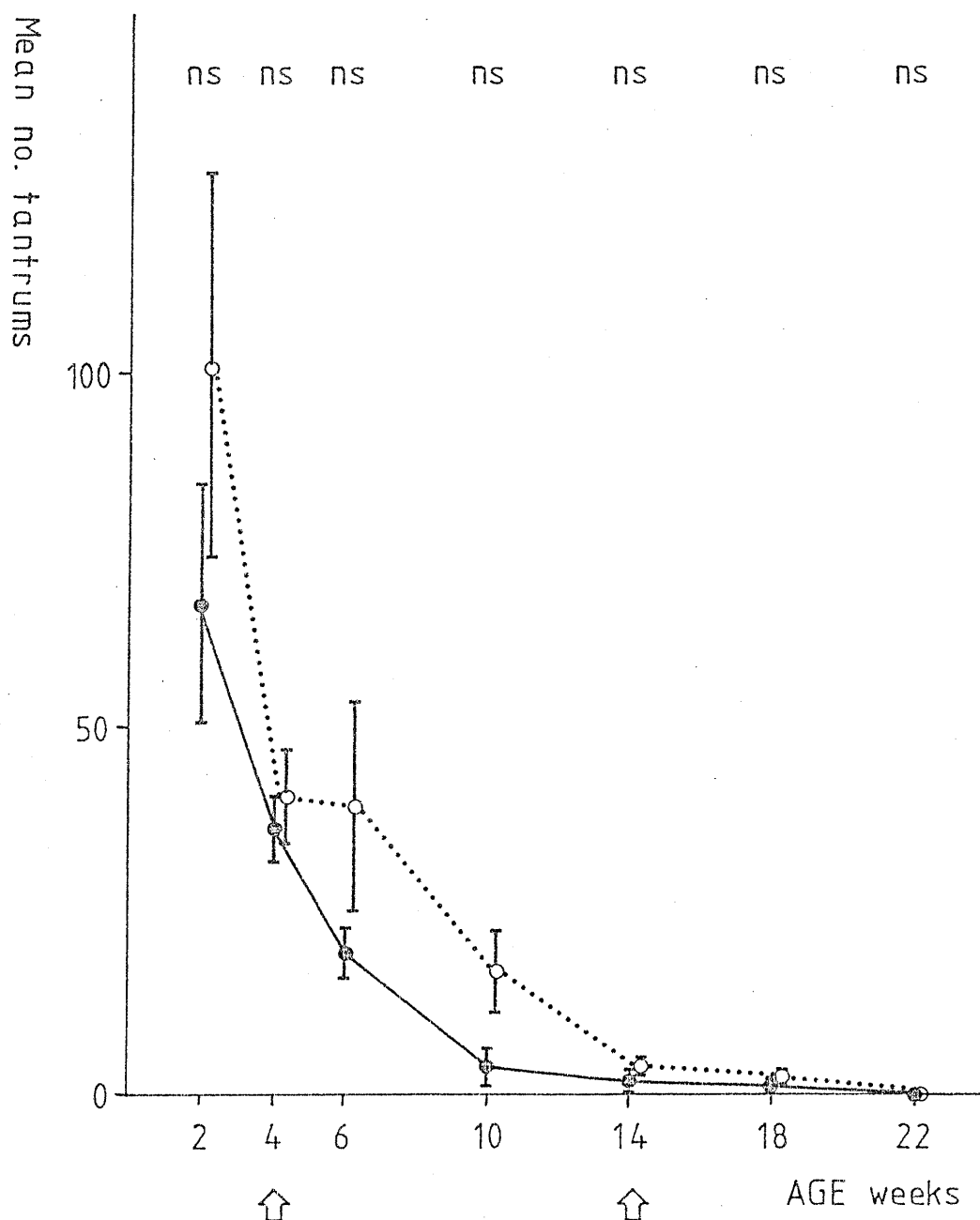


Figure 6.28

Mean total frequencies of tantrums shown by infants in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered.
Conventions as in figure 6.19.



interaction is sought at 14 weeks by an increase in the relative role of infants in maintaining proximity to caregivers.

Several of these changes were predicted: If the total care given is reduced the infant is expected to increase its care-seeking to make up the deficit. Non - care-seeking activities (play and off) become less important and the infant spends more time staying close to caregivers (huddling and maintaining proximity). The reduction in other activities which was found will be discussed in section 6.5).

b) Does the infant seek care differentially from different caregivers?

The second prediction from chapter 4 states that, with the drugged animal offering less care or social interaction to the infant, the infant will seek this from other caregivers and will seek it in order of preference. That is, if caregivers are rated differently with respect to the care they offer infants as was suggested by the results of Part I (sections 4.2) to 4.4)), the infant will seek most care from the highest rated caregiver and so on. If the results are unambiguous it should be possible to rank caregivers in order of their preference by the infant.

The first question to be investigated is whether or not infants respond to the altered behaviour of the drugged animals by seeking less care or interactions from them, and secondly to discover whether the infants seek care from other family members in order of preference.

i) Do infants seek less care from caregivers offering less care?

Figures 6.29 to 6.34 compare infants from Parts I and II in three care-seeking behaviours as they are shown towards fathers and siblings. These behaviours are the frequency of attempts to get on to the caregiver, the amount of time spent grooming the caregiver, and

the number of approaches to the caregiver.

Before drug administration began, i.e. at 2 weeks, there were no significant differences between Part I and Part II infants in any of the above behaviours.

Grooming of fathers and siblings occurs infrequently, varies in amount from infant to infant, and shows no significant differences between Parts I and II (figures 6.29 and 6.30).

Part II infants interact less with fathers and show fewer attempts to get on to them at 4 and 6 weeks, though the difference in attempts to get on is not significant (figure 6.31). There is a delay between the onset of reduction in care from fathers and the response of the infants; approaches by infants to fathers are not significantly fewer in Part II infants until they are 6 weeks old. In addition, Part II infants approach fathers significantly less at 10 weeks (figure 6.32).

Part II infants make significantly fewer attempts to get on to siblings at 6 weeks, but this is not the case at 14 weeks when the siblings are drugged (figure 6.33). This is probably due to the rather low number of attempts to get on to any caregiver made by infants of 14 weeks (figure 6.27). Approaching of siblings occurs less frequently in Part II than Part I infants, significantly so at 6 and 10 weeks (figure 6.34).

From the above it would appear that most of the significant changes in infants' behaviour seem to be associated with the reduction in care from fathers at 4 to 6 weeks, rather than the reduction in social interactions with siblings at 14 weeks. Changes in the behaviour of Part II infants towards siblings before 14 weeks (i.e. fewer attempts to get on at 6 weeks, fewer approaches at 4, 6 and 10 weeks) may be a result of the effects on infants' behaviour of drugging the father at 4 weeks. E.g. having experienced unresponsiveness from an important

Figure 6.29

Mean percentage of time infants spend grooming fathers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Probabilities refer to results of two-tailed Mann-Whitney U tests between data from Part I and Part II at each age.

*** $p < 0.002$. ** $p < 0.02$. * $p < 0.05$. ns non-significant.

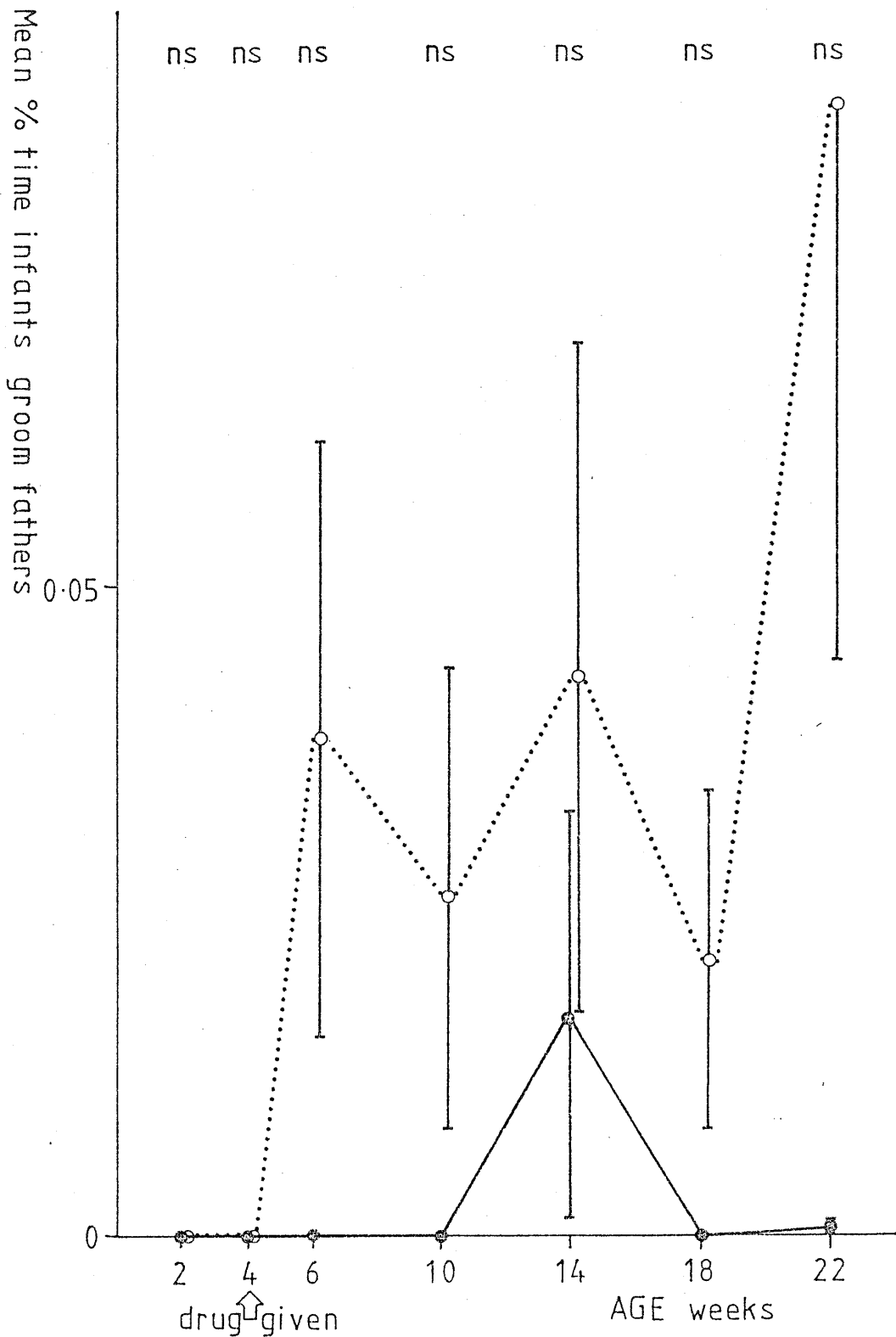


Figure 6.30

Mean percentage of time infants spend grooming siblings in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.29.

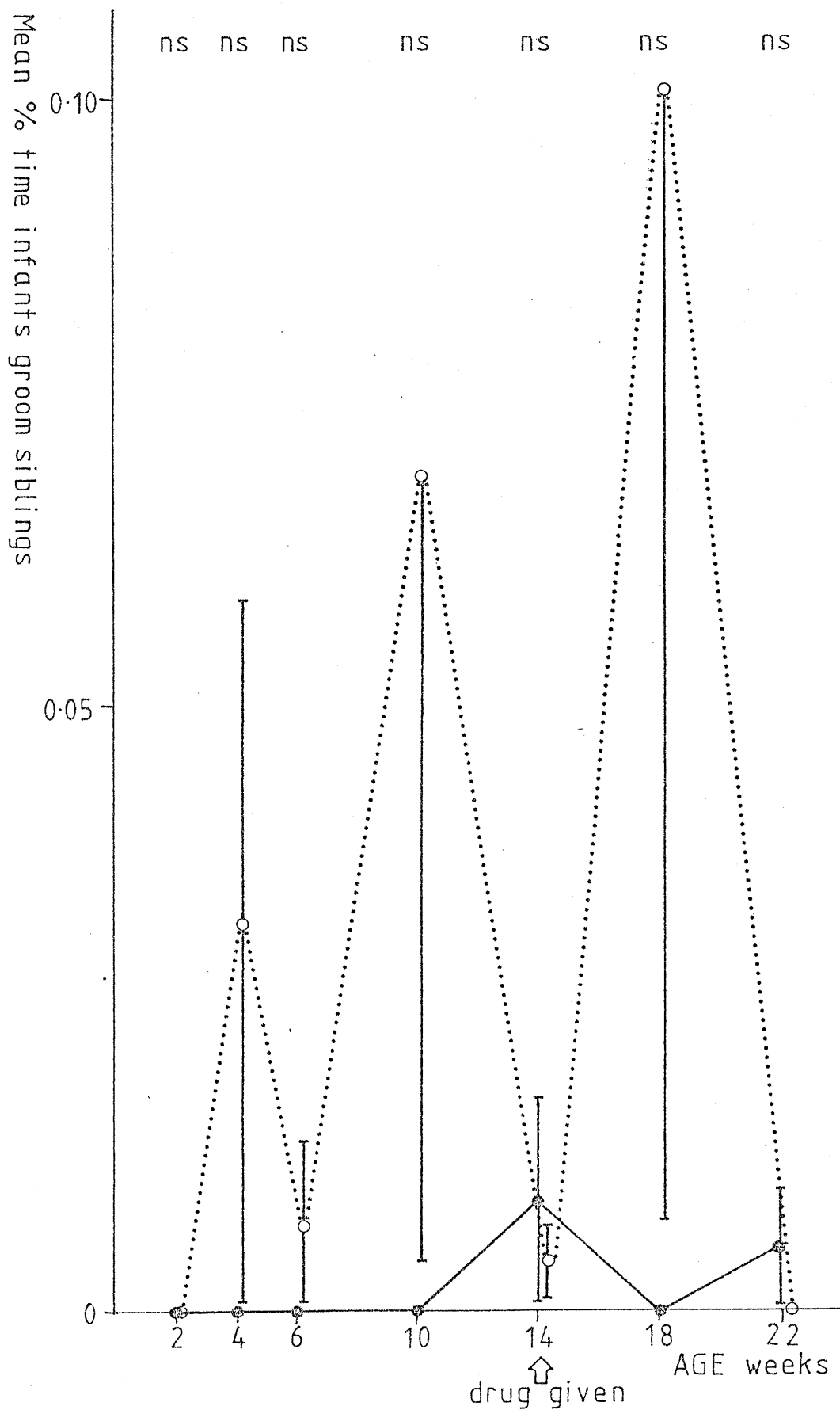


Figure 6.31

Mean frequency of attempts by infants to get on to fathers in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.29.

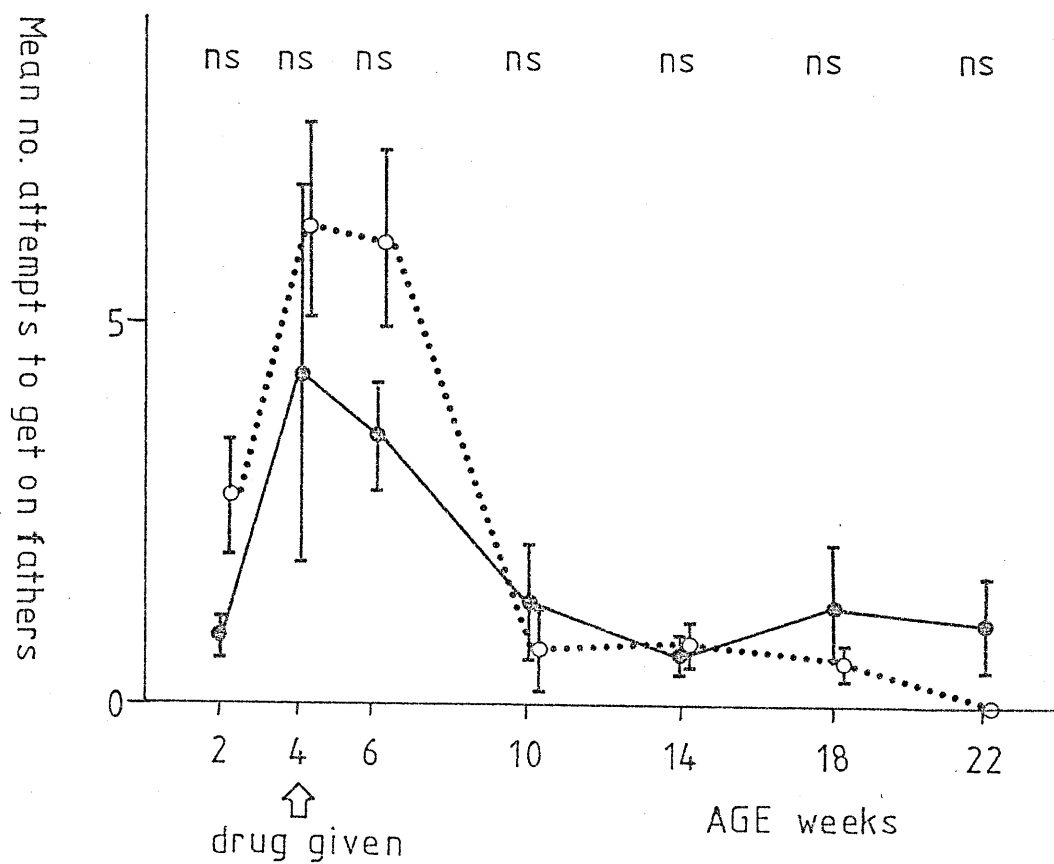


Figure 6.32

Mean frequency of approaches to fathers by infants in each Part of the study. Vertical lines denote standard errors.

□ Part I infants. ▨ Part II infants.

Conventions as in figure 6.29.

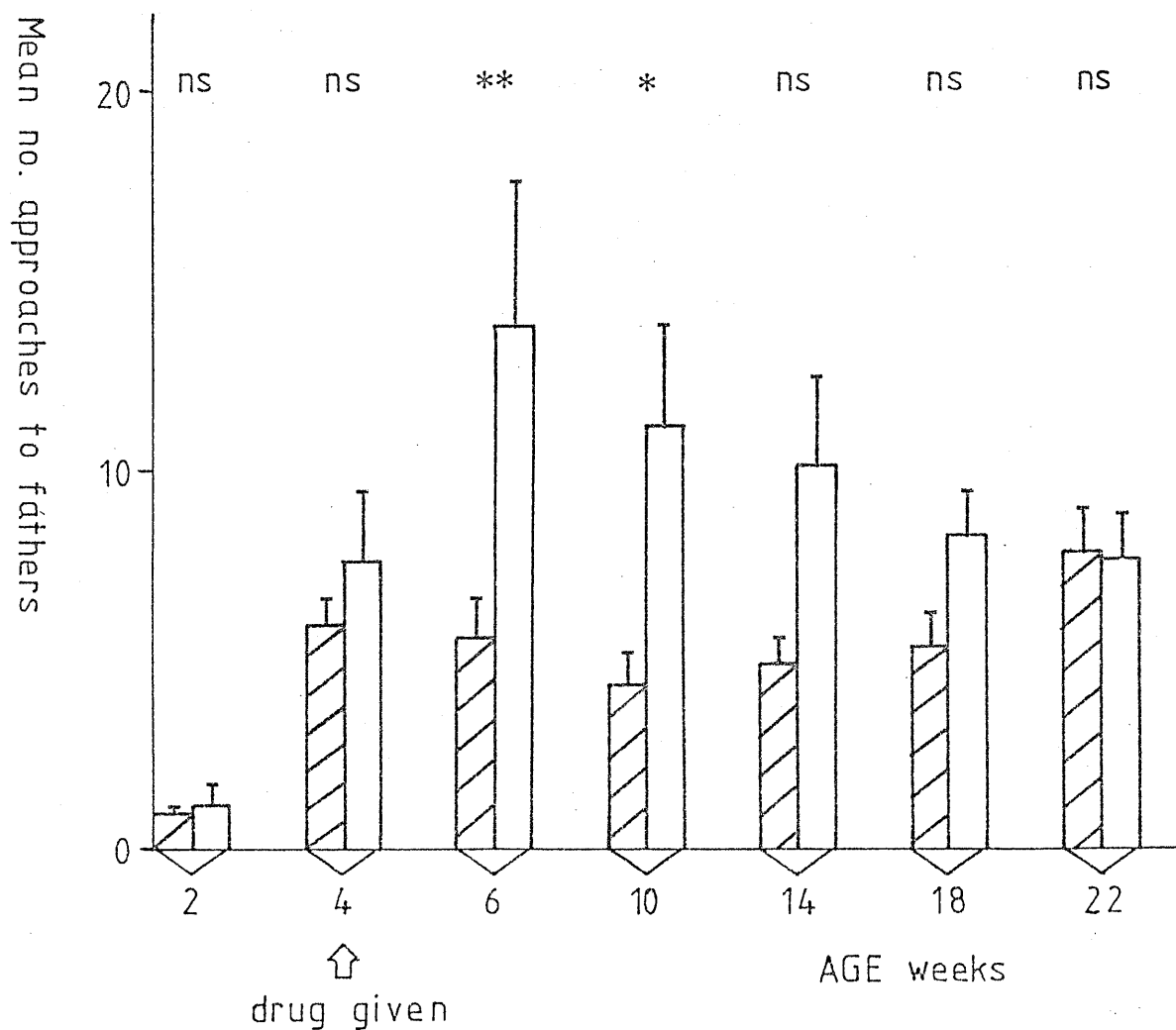


Figure 6.33

Mean frequency of attempts by infants to get on to siblings in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants.

Conventions as in figure 6.29.

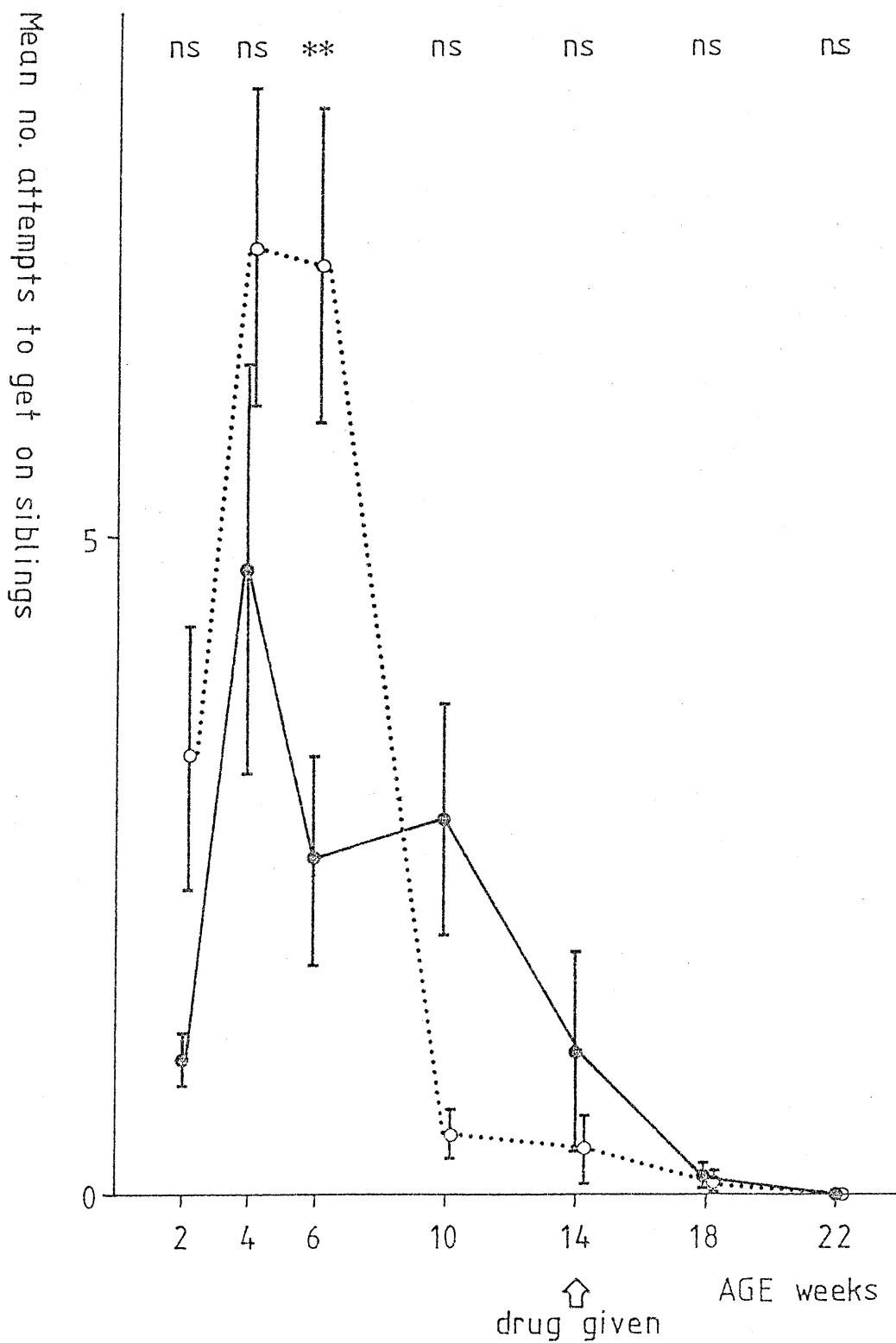
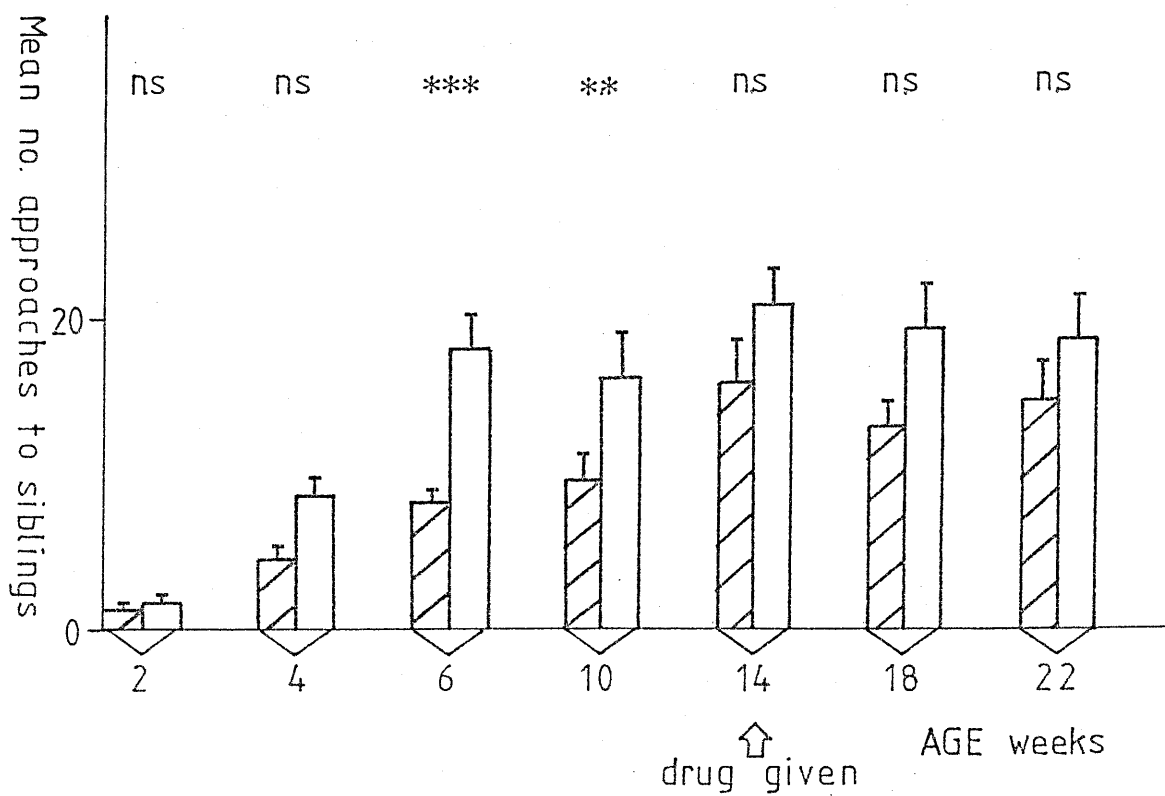


Figure 6.34

Mean frequency of approaches to siblings by infants in each Part of the study. Vertical lines denote standard errors.

□ Part I infants. ▨ Part II infants.

Conventions as in figure 6.29.



caregiver (important in terms of time normally spent with at these ages), infants may behave towards other, less important caregivers as though they were unresponsive also. This is an indication of the way social relationships form networks, in that altering one (father-infant) produces effects on others (sibling-infant).

There is therefore no evidence that infants seek social interaction less from siblings which are drugged when the infants are 14 weeks old. They do, however, alter their pattern of care-seeking after fathers are drugged at 4 weeks. Infants with fathers drugged at 4 weeks approach fathers less at 6 and 10 weeks, approach siblings less at 6 and 10 weeks, and attempt to get on to siblings less at 6 weeks when compared to infants whose fathers were not drugged.

ii) Is care sought from family members in order of preference?

Figures 6.35 to 6.38 show the distribution of Part II infants' various care-seeking behaviours amongst their caregivers. These figures suggest that, as for Part I infants, Part II infants differ markedly in the number of times they try to get on to different caregivers, in how much time they spend grooming different caregivers, and in how often they approach (and also leave) them. This uneven distribution of care-seeking directed towards different caregivers suggests that caregivers are rated differently with respect to the care they offer, and that infants should seek care from them in order of preference.

The detailed differences in care-seeking from different caregivers can be obtained from the figures (6.35 to 6.38) and from table 6.1 which indicates where these differences are significant. In summary, Part II infants make significantly more attempts to get on to mothers than on to any other caregivers at 6 and 10 weeks (figure 6.35), and direct significantly more grooming towards her than to others after 14 weeks (figure 6.36). Twins and siblings are approached

Figure 6.35

Mean number of attempts by infants to get on to different caregivers in Part II of the study. Vertical lines denote standard errors.

● father. ○ mother. ▲ siblings. ■ twin.

For significance of differences between caregivers at each age see table 6.1.

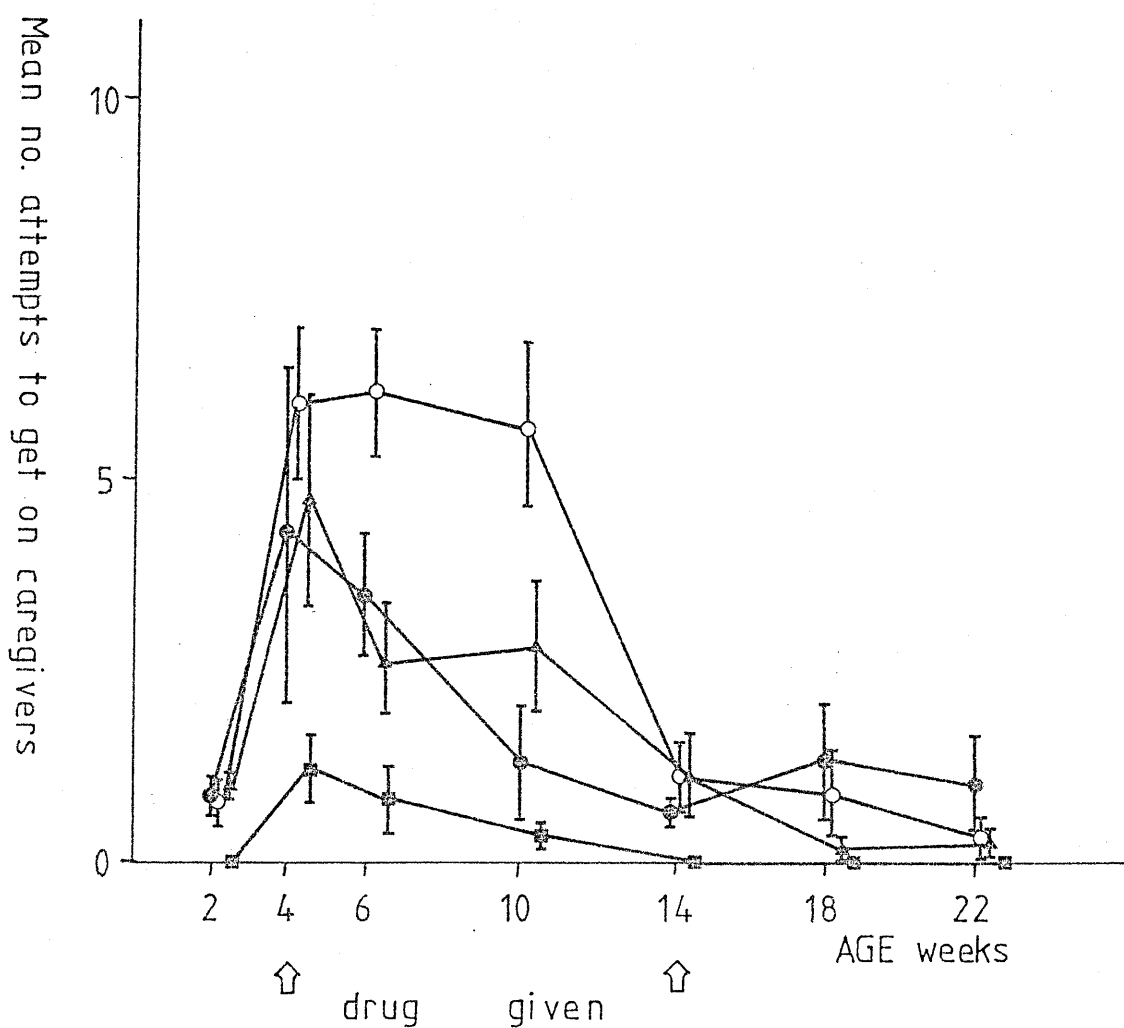


Figure 6.36

Mean percentage of time infants spend grooming different caregivers in Part II of the study. Vertical lines denote standard errors.

● father. ○ mother. ▲ siblings. ■ twin.

For significance of differences between caregivers at each age see table 6.1.

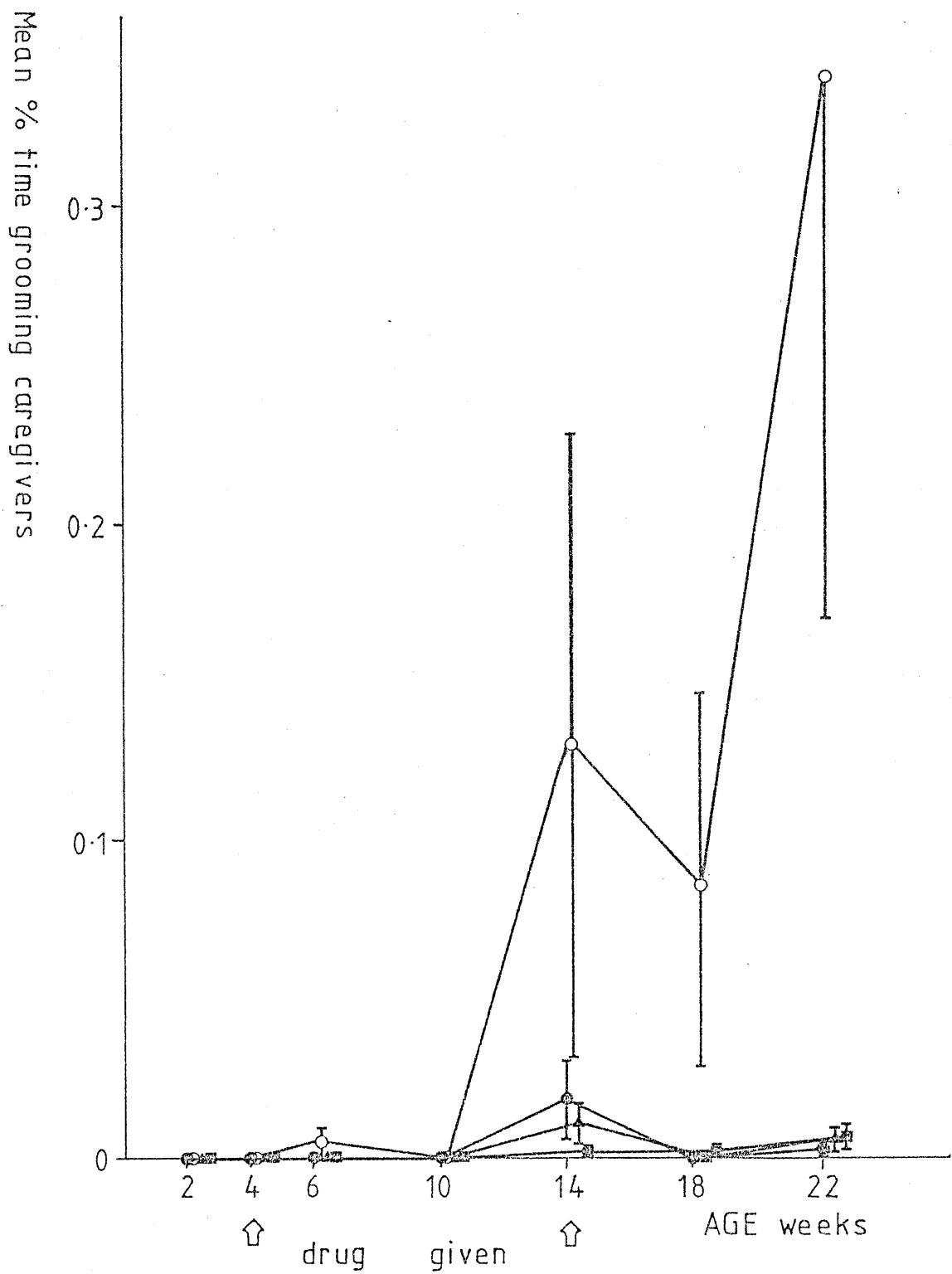


Figure 6.37

Mean frequencies of approaches by infants to different caregivers in Part II of the study. Vertical lines denote standard errors.

● father. ○ mother. ▲ siblings. ■ twin.

For significance of differences between caregivers at each age see table 6.1.

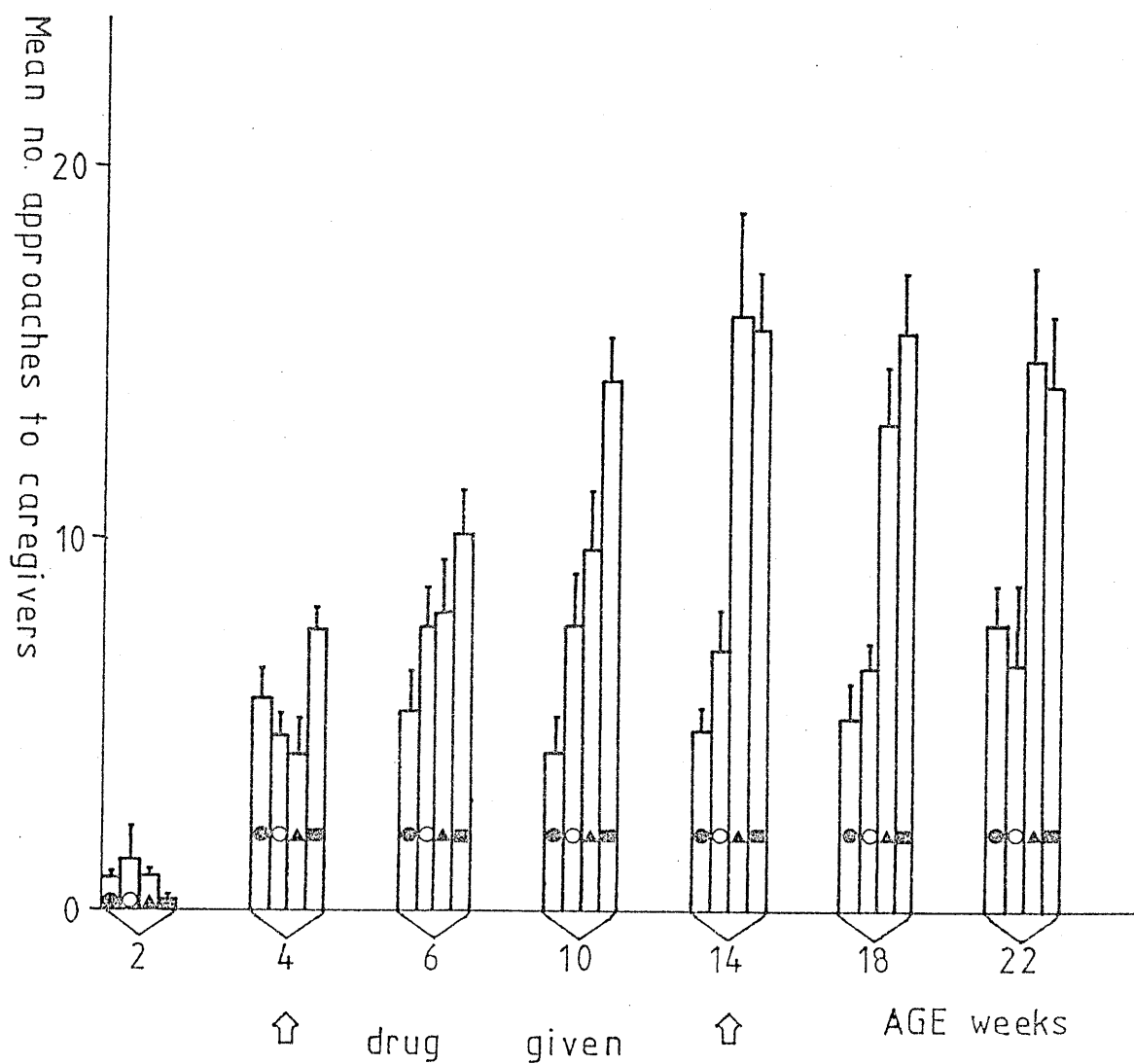


Figure 6.38

Mean frequencies of leavings by infants from different caregivers in Part II of the study. Vertical lines denote standard errors.

● father. ○ mother. ▲ siblings. ■ twin.

For significance of differences between caregivers at each age see table 6.1.

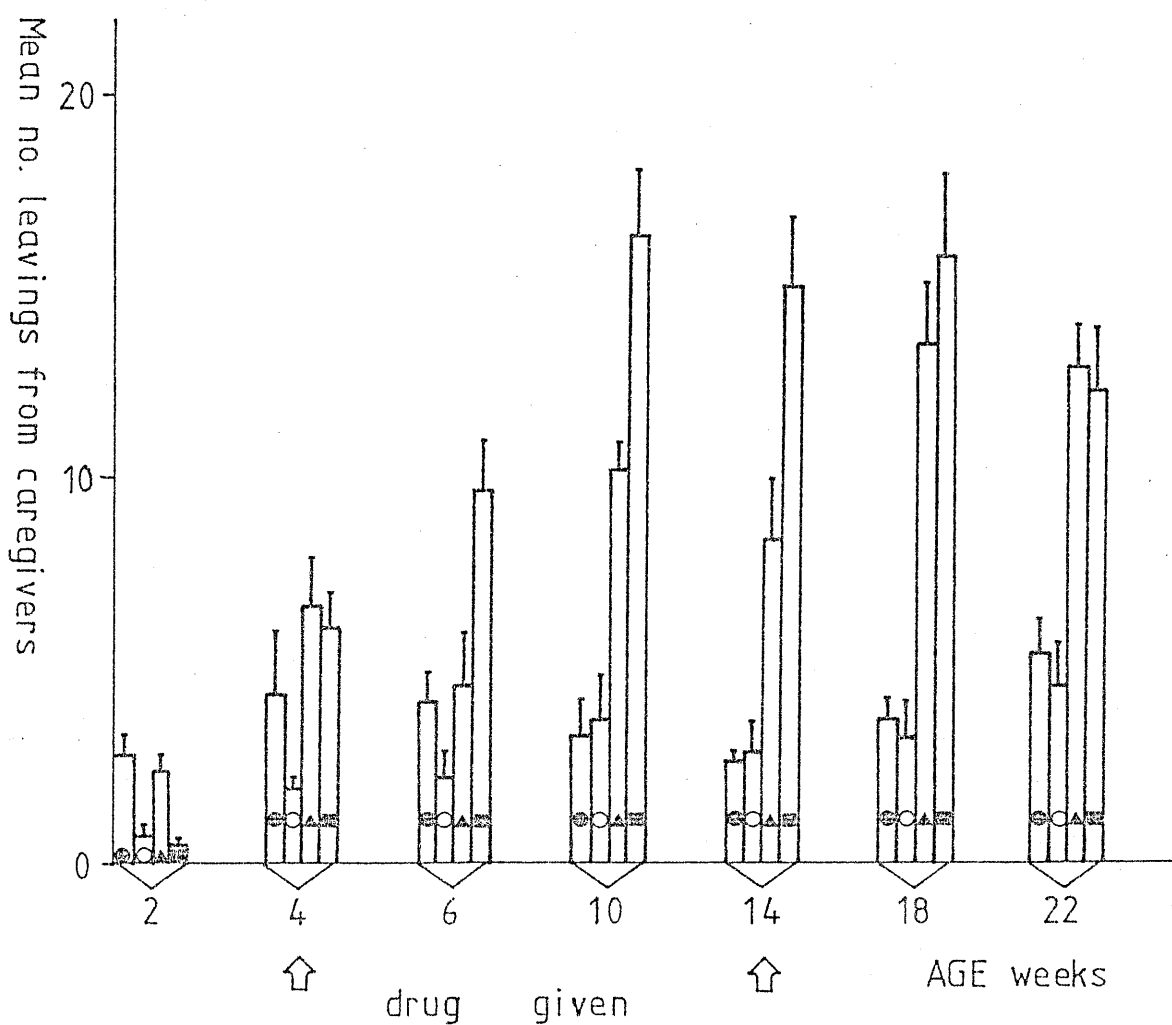


Table 6.1

Differences in various behaviours directed towards different caregivers by Part II infants at each age. Two-tailed randomization tests with a 5% significance level. ns not significant. * difference significant at $p < 0.05$. > more of behaviour directed at first caregiver in lefthand column. < more of behaviour directed at second caregiver.

CAREGIVER	AGE/weeks						
	2	4	6	10	14	18	22
Approaches To Caregiver							
Father vs mother	ns	ns	ns	ns	ns	ns	ns
Father vs sibs	ns	ns	ns	* <	* <	* <	* <
Father vs twin	* >	ns	* <	* <	* <	* <	* <
Mother vs sibs	ns	ns	ns	ns	* <	* <	* <
Mother vs twin	ns	* <	ns	* <	* <	* <	* <
Sibs vs twin	* >	* <	ns	* <	ns	ns	ns
Leavings From Caregiver							
Father vs mother	* >	ns	* >	ns	ns	ns	ns
Father vs sibs	ns	ns	ns	* <	ns	* <	* <
Father vs twin	* >	ns	* <	* <	* <	* <	* <
Mother vs sibs	* <	* <	* <	* <	ns	* <	* <
Mother vs twin	ns	* <	* <	* <	* <	* <	* <
Sibs vs twin	* >	ns	* <	* <	* <	ns	ns
Attempts To Get On							
Father vs mother	ns	ns	* <	* <	ns	ns	* >
Father vs sibs	ns	ns	ns	ns	ns	* >	ns
Father vs twin	* >	* >	* >	* >	* >	* >	* >
Mother vs sibs	ns	ns	* >	* >	ns	ns	ns
Mother vs twin	* >	* >	* >	* >	* >	* >	* >
Sibs vs twin	* >	* >	* >	* >	* >	* >	* >
Time Grooming Caregiver							
Father vs mother	ns	ns	* <	ns	ns	* <	* <
Father vs sibs	ns	ns	ns	ns	ns	ns	ns
Father vs twin	ns	ns	ns	ns	ns	* <	ns
Mother vs sibs	ns	ns	* >	ns	ns	* >	* >
Mother vs twin	ns	ns	* >	ns	ns	ns	* >
Sibs vs twin	ns	ns	ns	ns	ns	* <	ns

(and left) significantly more often than fathers or mothers from 6 and 14 weeks onwards respectively (figures 6.37 and 6.38).

The figures also show that the different care-seeking behaviours are themselves distributed differentially amongst caregivers, i.e. the different measures (attempts to get on, grooming and approaches) are not correlated with one another and it is therefore not possible to produce a single rank order of the preference of caregivers by infants. This is perhaps not surprising since there are many components of caregiving (see section 6.1)) and it is likely that infants will prefer different caregivers for different aspects of care. Figures 6.35 to 6.38 indicate that in the early weeks infants prefer to get on to mothers presumably for security and a chance to take milk, while preferring to interact actively (by frequent approaches and leavings) with twins. During later weeks mothers are groomed most, perhaps as a means to ensure some contact comfort now that the infants are too old to be carried, but twins and siblings are most often sought out in approach/withdrawal interactions.

Because different behaviours show different patterns of distribution among caregivers, to test whether or not reduced caregiving by particular individuals results in the infant seeking care from other family members in order of preference as predicted, it is necessary to select particular measures and compare the infants' ratings of caregivers with respect to these measures in Part I versus Part II.

At 4 weeks of age, Part II fathers pick up infants significantly less often than do Part I fathers (figure 6.3). An appropriate measure of care-seeking preference at this age therefore would be the number of attempts infants make to get on to different caregivers. However at 4 weeks there are no significant differences in the number of times infants attempt to get on to fathers, mothers or siblings (table 6.1).

This is also true of Part I infants (figure 4.19). There are therefore no clear preferences in terms of getting on to different caregivers in either Part of the study at this age.

Part II fathers also groom and approach infants significantly less often than do Part I fathers at 4 and 6 weeks (figures 6.4 and 6.9)), but again there are few significant differences in the grooming or approaching of caregivers by infants at these ages in either Part II (table 6.1) or Part I (sections 4.2c) and 4.3a)) and hence no significant preferences to compare between the two Parts.

It is possible however, to use as a measure of care-seeking preference the number of attempts infants make to get on to different caregivers at 6 weeks of age, when there are significant differences between different caregivers (table 6.1 and figures 6.35 and 4.19). This is not unreasonable since there may be a delay in the response of infants to reduced care from fathers (Part II infants do not begin to approach fathers significantly less often than Part I fathers until 6 weeks, see section 6.2b)), even though by 6 weeks Part II fathers are no longer picking up infants significantly less often than Part I fathers (figure 6.3).

Table 6.2 shows the mean number of attempts infants from both Parts of the study make to get on to each category of caregiver, together with the standard errors. Table 6.3 shows that in both Parts all differences between caregivers in the number of attempts to get on are significant except for that between fathers and siblings. The scores in table 6.2 are therefore ranked accordingly, with different ranks given only where the scores are significantly different. Scores which are not significantly different (ties) are given their average rank. These ranks are also shown in table 6.2.

Table 6.2 shows that the order of preference in Part I for

Table 6.2

Mean number of attempts (\pm standard error) made by infants to get on to different caregivers at 6 weeks of age in each Part of the study, together with their ranks. Caregiver which receives the most attempts to get on is given rank 1. Ties (non-significant difference between the number of attempts to get on) are given the average rank of the tied scores.

CAREGIVER	MEAN NO. ATTEMPTS TO GET ON \pm standard error		RANK	
	Part I	Part II	Part I	Part II
Father	6.00 \pm 1.22	3.50 \pm 0.73	2.5	2.5
Mother	10.62 \pm 1.06	6.12 \pm 0.97	1	1
Siblings	7.12 \pm 1.40	2.62 \pm 0.80	2.5	2.5
Twin	0	0.75 \pm 0.52	4	4

Table 6.3

Differences in the number of attempts infants make to get on to different caregivers at 6 weeks of age in each Part of the study. Two-tailed randomization tests with a 5% significance level. ns not significant.

* significant difference. > more attempts made with first caregiver in lefthand column. < more attempts made with second caregiver.

CAREGIVER	PART I	PART II
Father vs mother	* <	* <
Father vs siblings	ns	ns
Father vs twin	* >	* >
Mother vs siblings	* >	* >
Mother vs twin	* >	* >
Siblings vs twin	* >	* >

attempts by infants to get on to caregivers at 6 weeks is mothers > fathers/siblings > twins. In Part II the ranks are the same, infants are therefore in this instance seeking care (i.e. attempting to get on) in order of preference and not simply according to availability. If the latter were the case the ranks could be expected to be different in Part II since fathers are relatively less available (approaching and grooming infants significantly less) whereas twins are relatively more available (since they are experiencing the same reduction in care from fathers as are the infants).

At 14 weeks, Part II siblings spend less time with infants and approach them less than do Part I siblings (figures 6.11 and 6.17). Infants' preferences in approaching different caregivers in Part I versus Part II at this age are therefore examined.

Table 6.5 shows that differences in the number of approaches made by infants of both Parts to fathers and mothers, and to siblings and twins respectively are not significant and therefore their scores are treated as 'ties' in ranking the number of approaches made to each caregiver. For Part I and Part II this produces an order of preference as follows: Twins/siblings > mothers/fathers (table 6.4). Thus, in Part II when siblings are approaching infants less, playing with them less, spending less time with them and ignoring them more, infants continue to approach caregivers in the same order of preference as in Part I. This is perhaps not very meaningful since, due to the non-significant differences between numbers of approaches to some caregivers, there are effectively only two ranks. However the results are consistent with those given above for the number of attempts infants make to get on to caregivers at 6 weeks.

From the limited data available it would appear therefore that, as predicted by the hypothesis, infants continue to seek care (i.e.

Table 6.4

Mean number of approaches (\pm standard error) made by infants to different caregivers at 14 weeks of age in each Part of the study, together with their ranks. Caregivers which receive most approaches are given lowest rank. Ties (non-significant differences between numbers of approaches to different caregivers) are given the average rank of the tied scores.

CAREGIVER	MEAN NO. APPROACHES TO CAREGIVER \pm standard error		RANK	
	Part I	Part II	Part I	Part II
Father	10.00 \pm 2.52	4.87 \pm 0.76	3.5	3.5
Mother	17.75 \pm 5.64	7.00 \pm 1.19	3.5	3.5
Siblings	21.12 \pm 2.30	16.00 \pm 3.00	1.5	1.5
Twin	25.00 \pm 5.64	15.75 \pm 1.68	1.5	1.5

Table 6.5

Differences in the number of approaches infants make to different caregivers at 14 weeks in each Part of the study. Two-tailed randomization tests with a 5% significance level. ns not significant. * significant difference. > more approaches made to first caregiver in lefthand column. < more approaches made to second caregiver,

CAREGIVER	PART I	PART II
Father vs mother	ns	ns
Father vs siblings	* <	* <
Father vs twin	* <	* <
Mother vs siblings	* <	* <
Mother vs twin	* <	* <
Siblings vs twin	ns	ns

attempt to get on, approach) in their normal (i.e. undrugged) order of preference when care from particular individuals is altered by drug administration.

c) Does compensation occur in caregiving behaviour?

The third and fourth predictions of the caregiving/care-seeking hypothesis are concerned with whether or not compensation would occur to make up for the deficiencies in the caregiving behaviour of drugged animals.

Section 4.5d) suggested that in the case of the Part I animals, parents and siblings did not appear to compensate for differences in each others' behaviour towards infants. By contrast, twins in some cases did appear to compensate; for example twins spent more time with infants of more rejecting parents than with infants of less rejecting parents.

The caregiving/care-seeking hypothesis (section 4.9) suggests that where the total amount of care available to the infants exceeds that required by the infants, compensation could be expected to occur as the more caring individuals make up for low amounts of care offered by less caring members of the group. This would occur automatically assuming individuals differ in the amounts of care they are prepared to give and would not depend on animals 'consciously' responding to other animals caregiving levels.

Under the drug-modified conditions of Part II the total amount of care available to the infant is reduced so it is even less likely to exceed the infant's requirements than in Part I. Compensation might not therefore be expected to occur, unless caregivers actually perceive a deficiency in the drugged animal's behaviour and relate this to their own care of the infant as occurs in the case of humans (e.g. see Rutter, 1972). If caregivers do not compensate, the amount of care from

different caregivers in Part II (excluding the drugged individuals) is expected to be in the same relative proportions as in Part I. Conversely, if some caregivers compensate, those caregivers will give proportionately and absolutely more care than in Part I. If all caregivers compensate to exactly the same extent, the proportions of care given will not change between Part's I and II but Part II absolute values of care given will be greater.

The prediction that compensation is not expected to occur in Part II is therefore investigated by examining the absolute amounts and relative proportions of different caregiving behaviours shown by caregivers from Part I and from Part II at the ages at which care has been shown to be reduced in the drugged animals (see section 6.2).

Figures 6.39 to 6.44 show the absolute amounts of care (frequencies or durations) shown by mothers, siblings and twins at 4 and 6 weeks, and by fathers, mothers and twins at 14 weeks for the following behaviours: Time spent with infant, time spent carrying infant, time spent in contact with infant, time spent grooming infant, number of approaches to infant, and frequency of picking up infant. For time spent carrying infant and the number of times infants are picked up there are insufficient data at 14 weeks for histograms to be drawn. Absolute amounts of care given by each category of caregiver in Part I versus Part II are compared using two-tailed Mann-Whitney U tests with a 5% significance level.

The figures show that there are no significant differences between Part I and Part II caregivers in the amount of time they spend with infants, in time spent carrying infants, in time in contact with infants, in time spent grooming infants, or in the number of times infants are picked up. In the case of approaches to infants, Part II twins approach infants significantly less often than do Part I twins

Figure 6.39

Mean percentage of time different caregivers spend with infants at different ages in each Part of the study. See text for details.

Vertical lines denote standard errors.

□ Part I infants. ■ Part II infants.

Two-tailed Mann-Whitney U tests carried out on data from Part I versus Part II: ns indicates non-significant difference, * indicates $p < 0.05$.

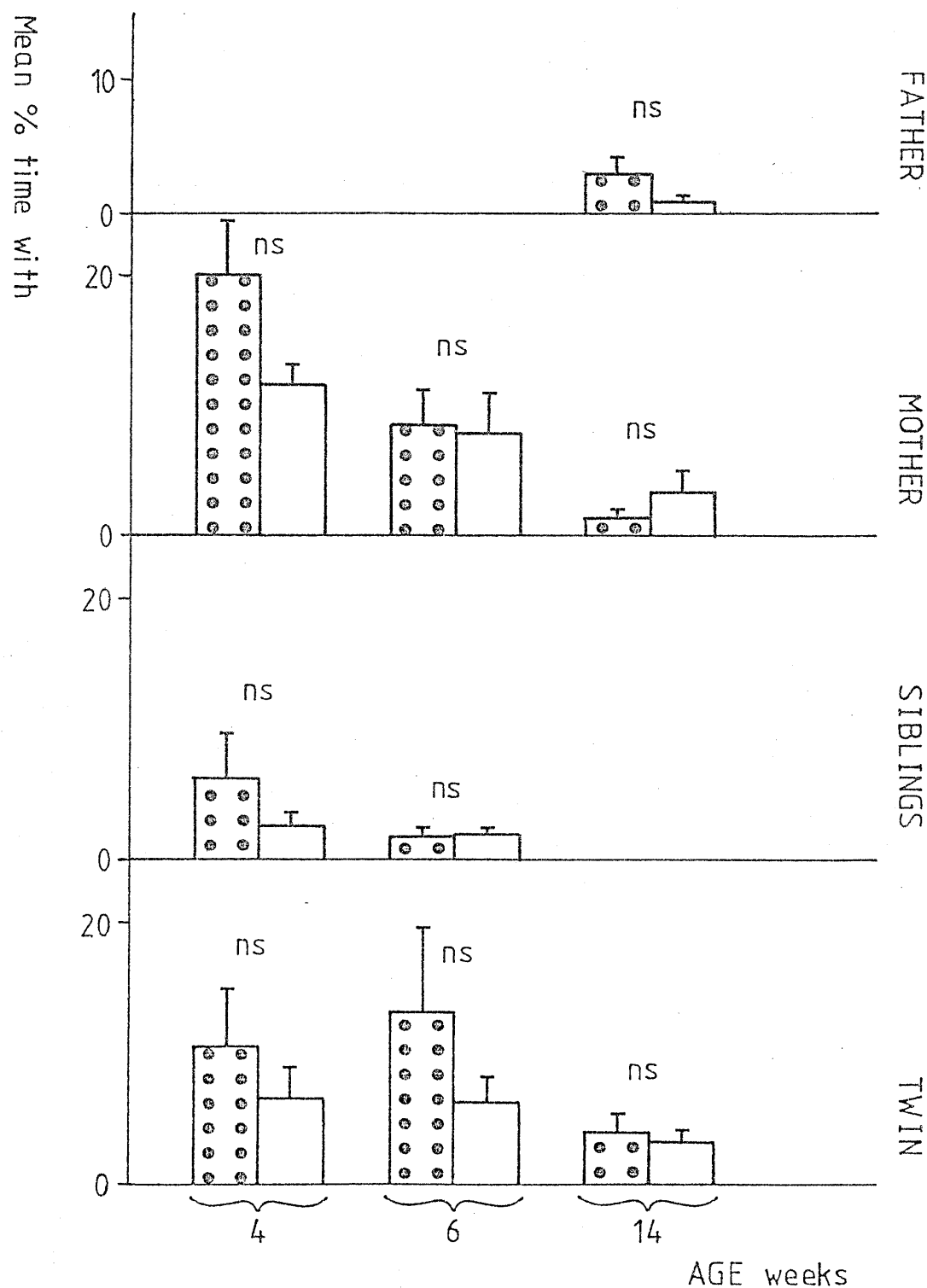


Figure 6.40

Mean percentage of time different caregivers spend carrying infants at different ages in each Part of the study. See text for details.

Vertical lines denote standard errors.

Part I infants. Part II infants.

Conventions as in figure 6.39.

(Part I twins do not carry infants.)

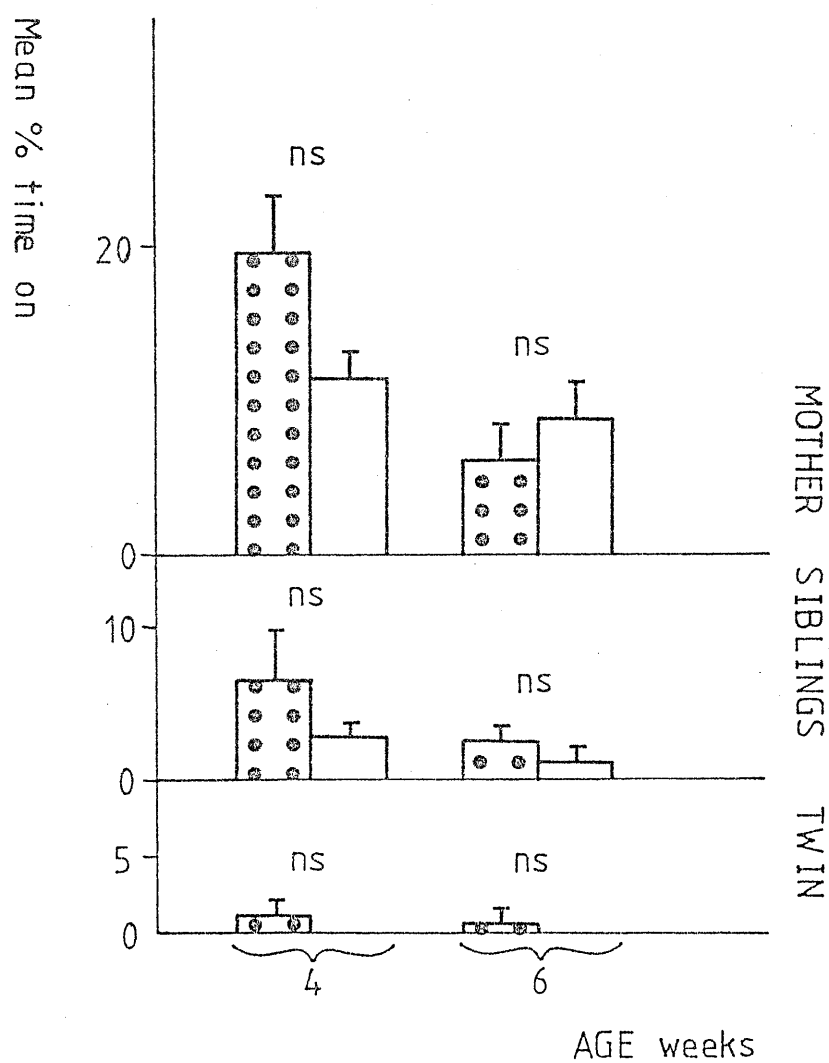


Figure 6.41

Mean percentage of time different caregivers spend in contact with infants at different ages in each Part of the study. See text for details. Vertical lines denote standard errors.

□ Part I infants. ■ Part II infants.

Conventions as in figure 6.39. Note different scale for twin.

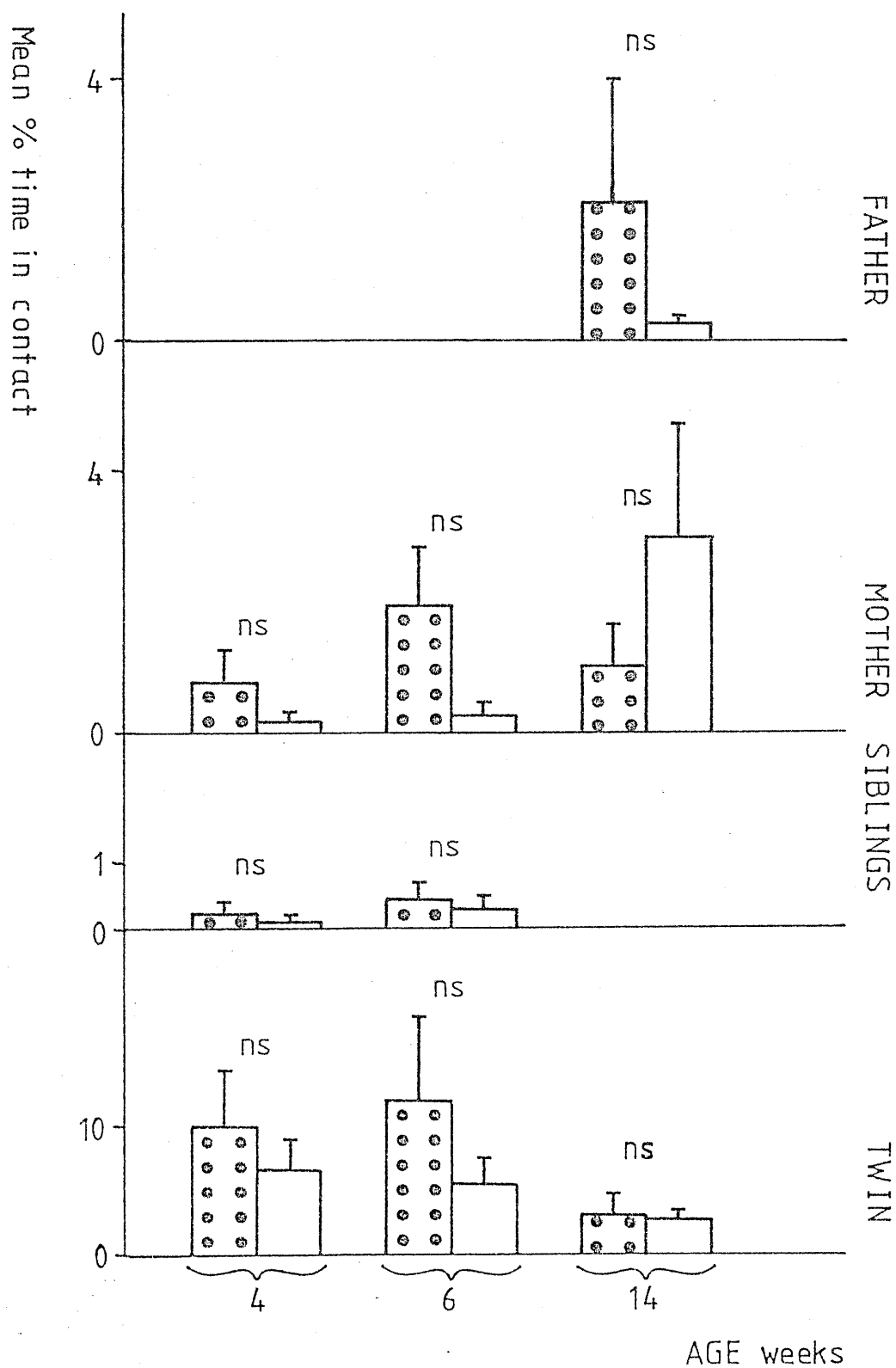


Figure 6.42

Mean percentage of time different caregivers spend grooming infants at different ages in each Part of the study. See text for details.

Vertical lines denote standard errors.

□ Part I infants. ◻ ◻ Part II infants.

Conventions as in figure 6.39.

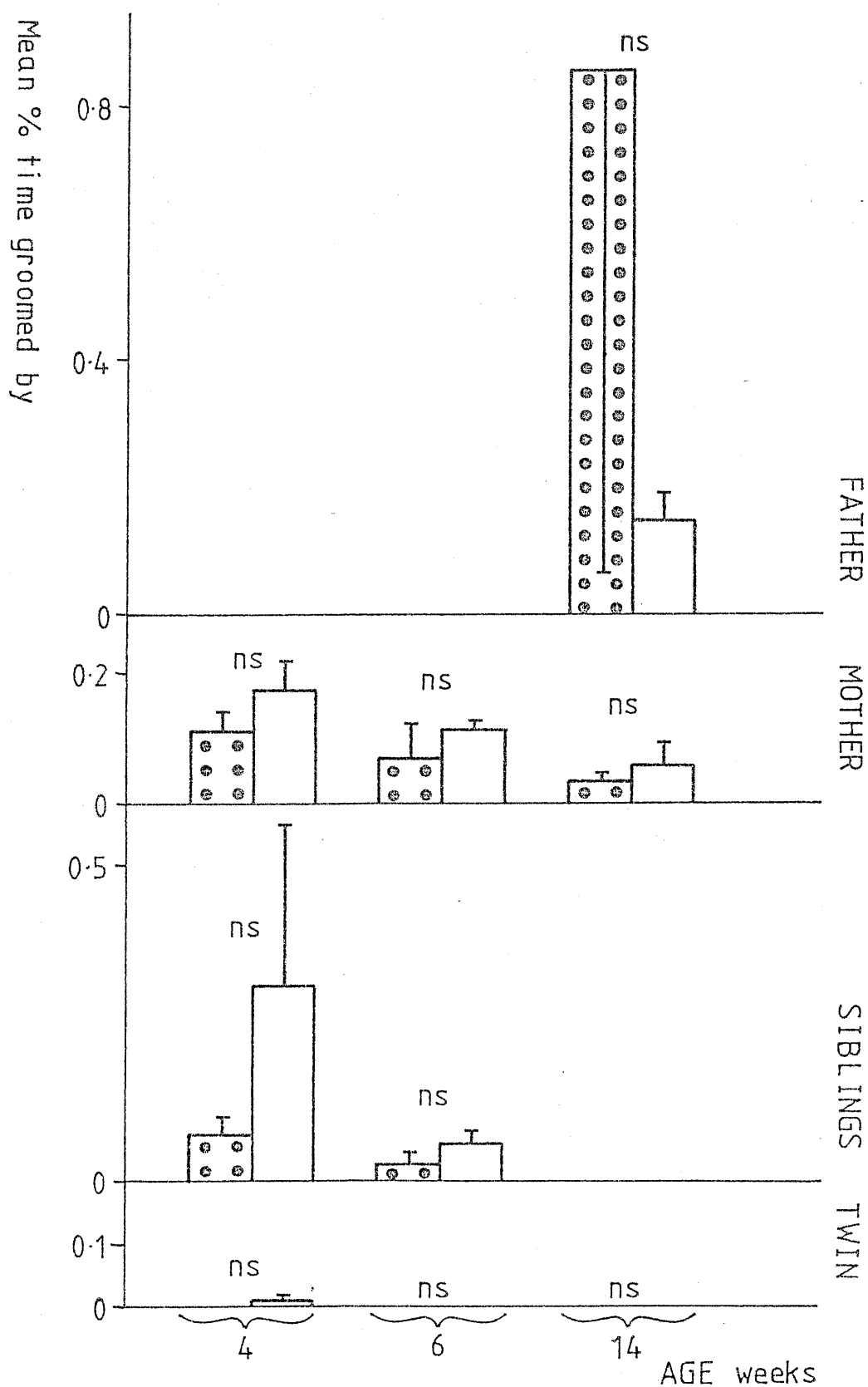


Figure 6.43

Mean frequency with which different caregivers approach infants at different ages in each Part of the study. See text for details.

Vertical lines denote standard errors.

□ Part I infants. ■ Part II infants.

Conventions as in figure 6.39.

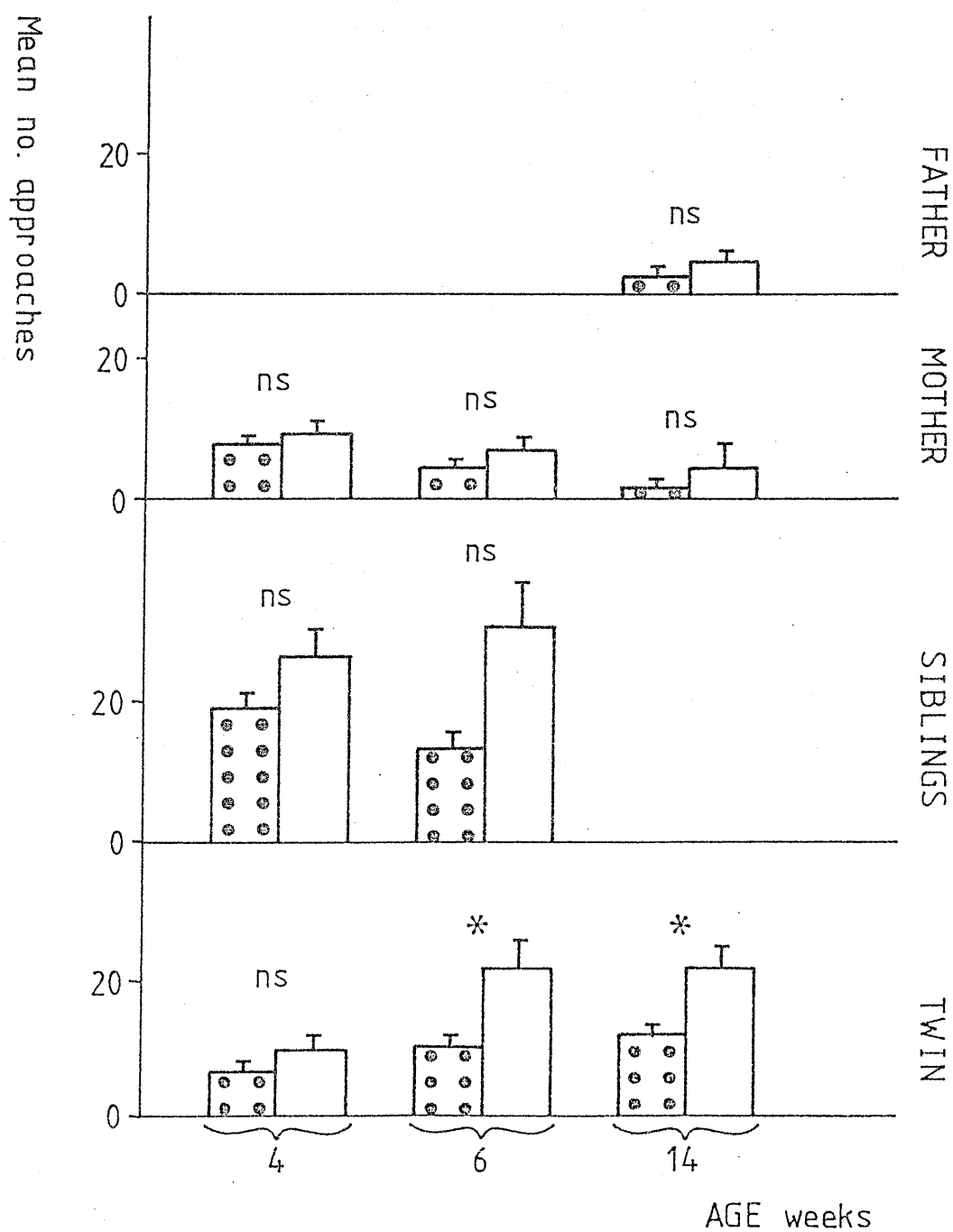


Figure 6.44

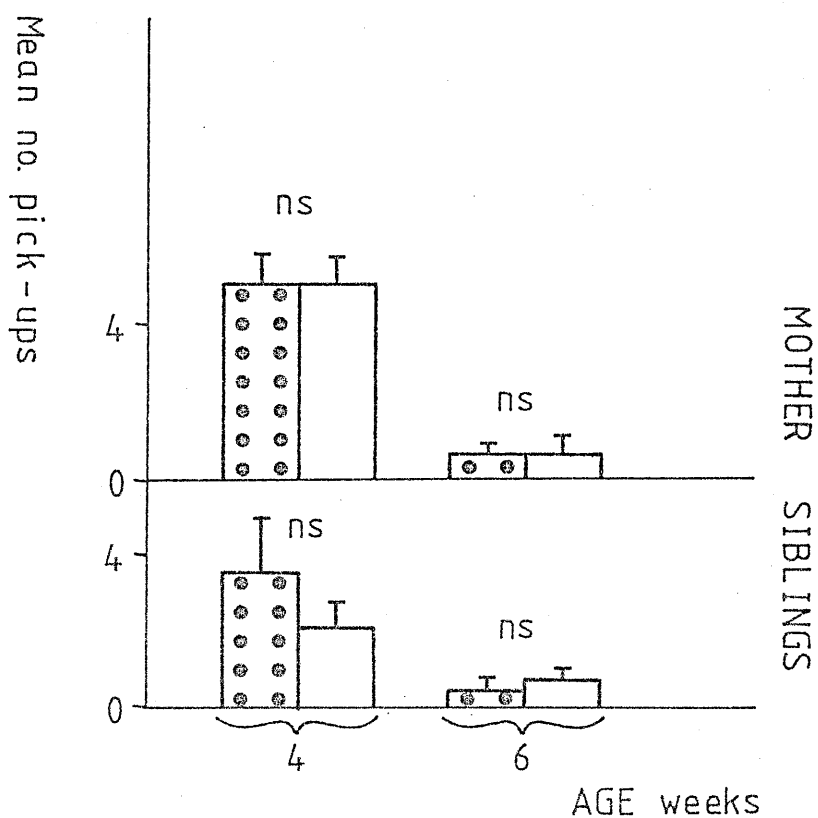
Mean frequency with which different caregivers pick up infants at different ages in each Part of the study. See text for details.

Vertical lines denote standard errors.

Part I infants. Part II infants.

Conventions as in figure 6.39.

(Twins do not pick up infants.)



at 6 and 14 weeks. Other differences in approaches to infants are not significant.

In no case therefore is the absolute amount of care from a caregiver in Part II significantly greater than that from that caregiver in Part I.

Figures 6.45 to 6.50 show the relative proportions of care shown by mothers, siblings and twins at 4 and 6 weeks, and by fathers, mothers and twins at 14 weeks for the same behaviours as above. Again there are insufficient data for time spent carrying infants and number of times infants are picked up at 14 weeks for histograms to be drawn. In the figures, data from caregivers of Part I infants are shown to the left of each histogram, Part II caregivers to the right. Relative proportions of care by each category of caregiver in Part I versus Part II are compared using two-tailed Mann-Whitney U tests with a 5% significance level.

The figures show that for all the above behaviours, the relative proportions of care shown by different caregivers in Part I are very similar to those shown in Part II. Mann-Whitney U tests revealed no significant differences between proportions shown by any caregiver in any of the behaviours.

Since the relative proportions of care given do not differ significantly between Part's I and II, and since absolute amounts of care given are in no case significantly greater in Part II than Part I, it can be concluded that compensation by other caregivers has not occurred to make up for reduced care from drugged animals in Part II. This is in agreement with the caregiving/care-seeking hypothesis and also indicates that marmoset caregivers either do not perceive, or do not respond (by increasing their own care levels), to small reductions in the amount of care given to infants by other members of their family.

Mean relative proportions of time different caregivers spend with infants at different ages in each Part of the study. See text for details.

I Part I infants. II Part II infants.

Two-tailed Mann-Whitney U tests carried out between proportions from different categories of caregiver in Part I versus Part II: ns indicates non-significant difference.



Mean relative proportions of time different caregivers spend carrying infants at different ages in each Part of the study. See text for details. Vertical lines denote standard errors.

Conventions as in figure 6.45.



Figure 6.47

Mean relative proportions of time different caregivers spend in contact with infants at different ages in each Part of the study. See text for details. Vertical lines denote standard errors.

I Part I infants. II Part II infants.

Conventions as in figure 6.45.

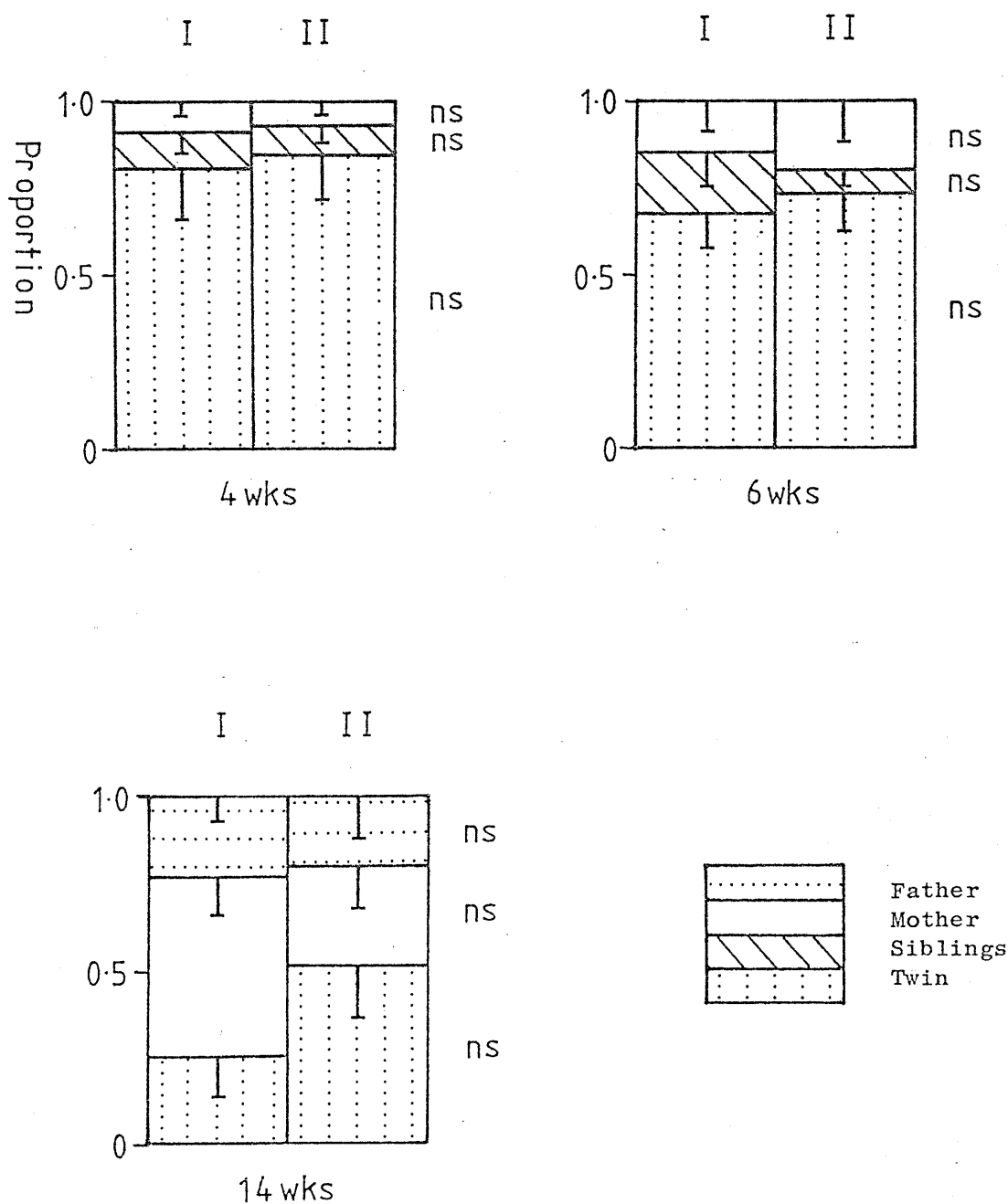


Figure 6.48

Mean relative proportions of time different caregivers spend grooming infants at different ages in each Part of the study. See text for details. Vertical lines denote standard errors.

I Part I infants. II Part II infants.

Conventions as in figure 6.45.

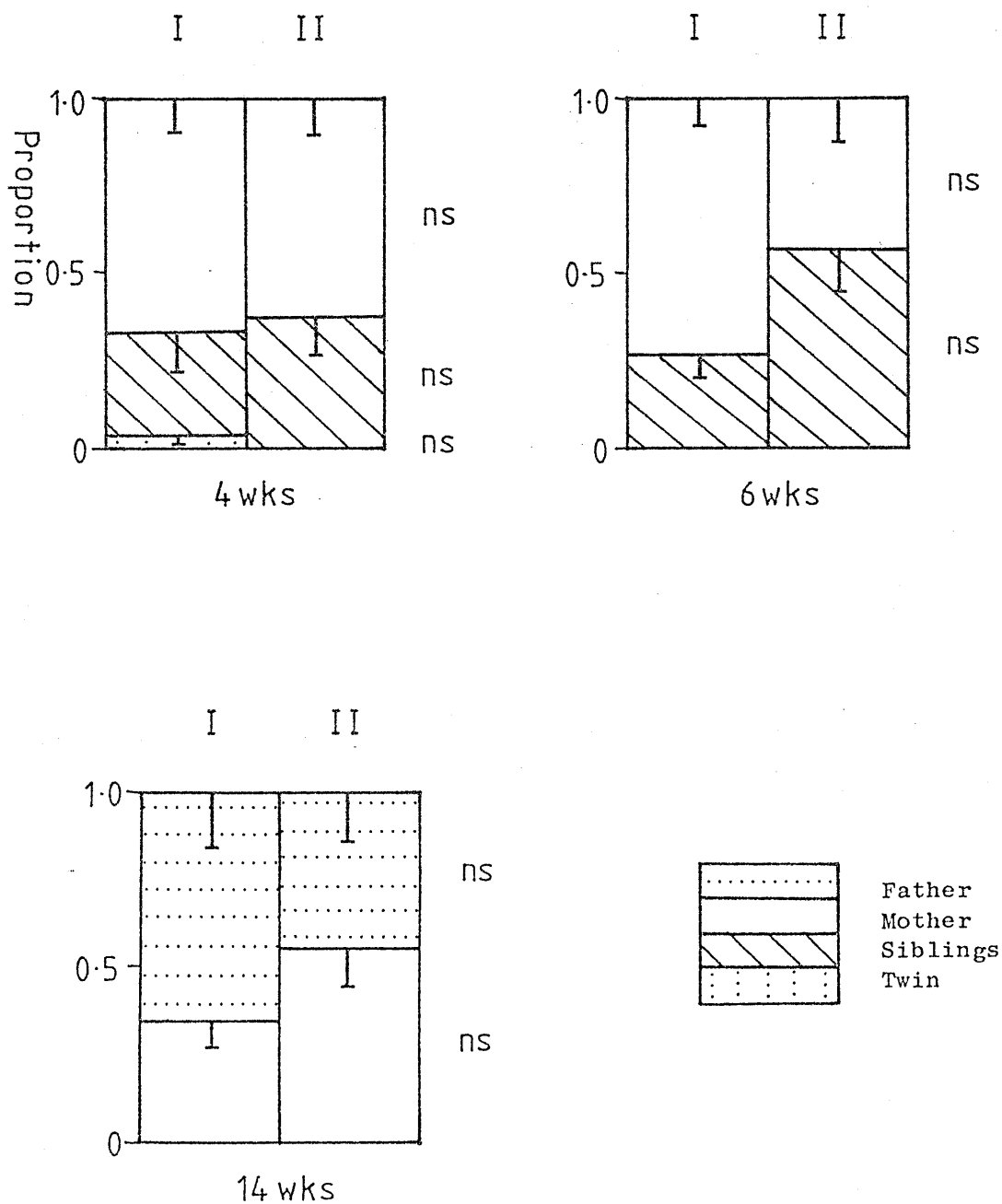


Figure 6.49

Mean relative proportions of approaches by different caregivers to infants at different ages in each Part of the study. See text for details. Vertical lines denote standard errors.

I Part I infants. II Part II infants.

Conventions as in figure 6.45.

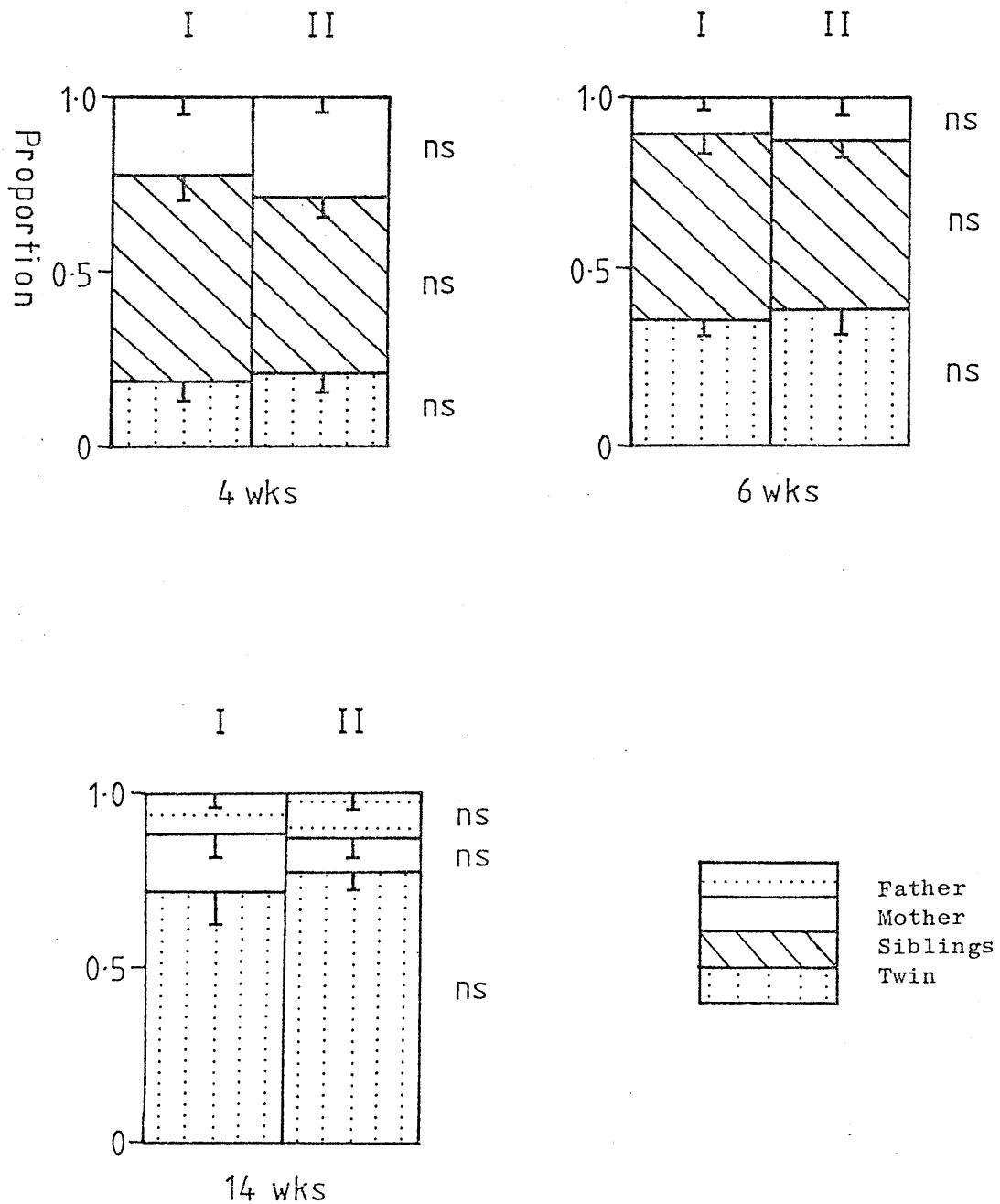


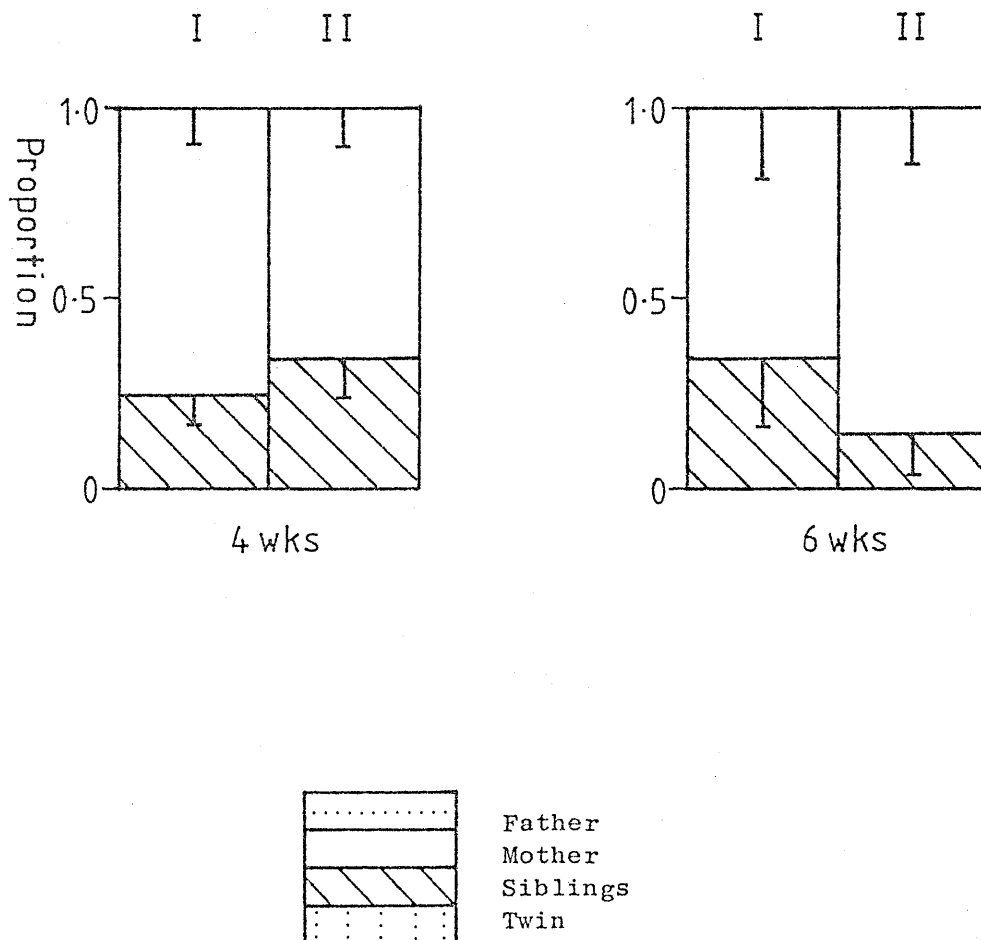
Figure 6.50

Mean relative proportions of frequency with which different caregivers pick up infants at different ages in each Part of the study. See text for details. Vertical lines denote standard errors.

I Part I infants. II Part II infants.

Conventions as in figure 6.45.

(Twins do not pick up infants.)



d) Do caregivers have a maximum level of care they are prepared to give?

It was suggested in section 4.9) that caregivers could be expected to have a 'normal maximum' level of care which they are prepared to give to infants at each age. This is also to be expected from the fact that families are quite capable of raising two infants at a time but can only rarely raise three (see chapter 2). If this maximum level is close to being reached in the undisturbed situation (Part I) and compensation does not occur (see above), then when the total amount of care available to the infant is reduced (in Part II) the infant would be expected to spend a total of more time off and in family huddles, behaviour states which require no positive care (i.e. effort expended) on the part of the caregivers.

At first sight this appears to be in contradiction to the first prediction of section 4.9) (and see section 6.3a)), in which less time off was indicated. This is a consequence of the two predictions dealing with different aspects of the hypothesis, i.e. care offered (in this section) and care sought (in section 6.3a)). The apparent contradiction is resolved as follows. In chapter 3 where the behaviour categories used in this study are defined, the infant's time is divided into four mutually exclusive states (on, off, huddle and contact) with the implication that the infant must be in one or other of these states at any given time. On and contact are caregiving behaviours (see section 6.1)). Therefore, if care given by specific individuals is reduced, and other caregivers are giving care at their 'normal maximum' levels (i.e. they will not increase the care they are giving), then the time spent in the remaining non-care behaviour states (off plus huddle) must necessarily increase to balance any decrease in time on and in contact. Hence it is logical, from the point of view of the present section, to predict an increase in off-plus-huddling, even though elsewhere time off (as a non - care-seeking activity) is predicted to decrease.

Figures 6.20 and 6.24 show the total percentage of time infants

spend off and away from caregivers at each age, and the total percentage of time spent in family huddles respectively. Part II infants spend significantly less time off caregivers at 4 and 6 weeks than do Part I infants, rather than more time off (see section 6.3a)), and there are no significant differences between Part's I and II at any other ages in this behaviour. Part II infants do however spend significantly more time huddling than Part I infants at 4 weeks of age, i.e. when fathers are drugged.

Figure 6.51 shows the mean combined totals of time off plus time huddling at each age for Part I and Part II infants and shows that there are no significant differences between Part I and Part II at any age, nor is the direction of the differences between the two Parts consistent over all ages.

It is possible therefore that close to the maximum level of care is being given by caregivers at 4 weeks and infants which spend less time with fathers which are drugged make up for this by spending more time in family huddles. Nevertheless, the results given in figure 6.51 do not show the predicted increase in time off-plus-huddling for Part II infants.

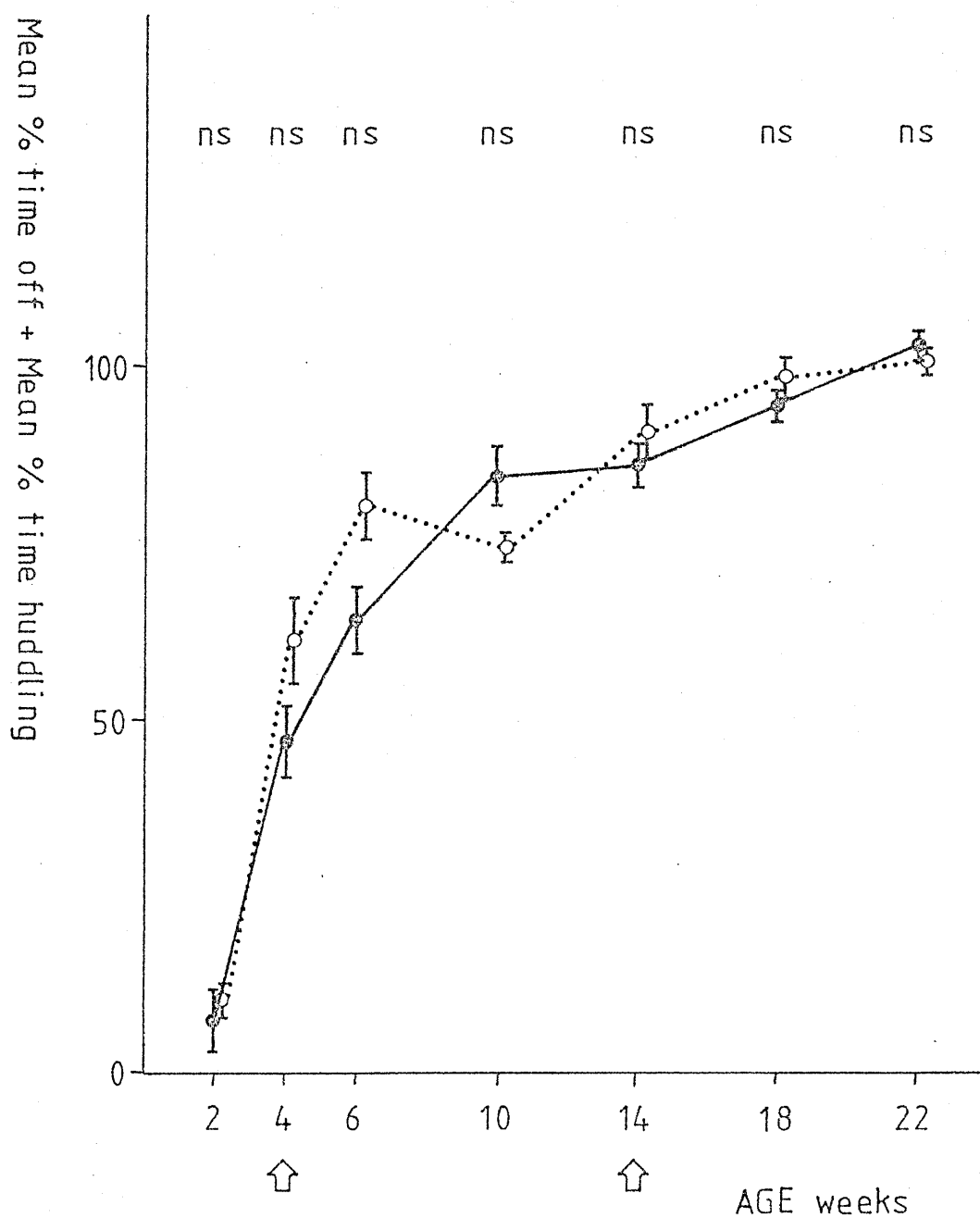
One explanation is that families in these captive conditions do not have to give as much care as their 'normal maximum' level since living conditions are less strenuous than in the wild. Individuals do not have to forage for food or search for safe sleeping sites, and therefore in captivity probably have more 'spare time' which they could devote to infants. At the same time infants will need less care than they would in the wild. They need no protection from predators and do not have to be prevented from moving too far away from caregivers or out of the territory.

To investigate the question of maximum care further it would

Figure 6.51

Mean total percentage of time infants spend off plus time spent huddling in each Part of the study. Vertical lines denote standard errors.

..... Part I infants. — Part II infants. ⇨ drug administered.
ns denotes non-significant difference between results of Part I versus Part II at age indicated (Mann-Whitney U tests).



be necessary either to reduce the care available more severely or to produce a captive environment that is more realistic and more difficult to live in.

e) Do infants become independent earlier if the care available to them is reduced?

It has been suggested by several workers (Hansen, 1966; Hinde & Spencer-Booth, 1967a & 1968; Jensen et al, 1969 & 1973) that caregivers regulate the development of their infants' independence by increasingly rejecting them and gradually giving less care and attention, and that the infant responds to this by directing more of its activities to its peers and to the environment and less to its principal caregivers. This has been shown to occur in human children, where mothers encourage children to try new experiences (solid food, language, walking etc.) before the child could or would make the choice itself, where they facilitate children's attempts to explore the environment and provide them with opportunities for achievements a little beyond their current accomplishments (Ainsworth, 1969; Hinde, 1979; Trevarthen, 1977). If this is the case in marmosets it could be expected that when care is reduced more than usual infants would become independent earlier.

From the present data this does not appear to be the case. Independence could be expected to be manifest in the amount of time infants spend off (i.e. away from caregivers and on their own, see chapter 3 for full definition). However infants receiving less care from caregivers (Part II) do not spend an increased amount of time off earlier than normally-cared-for infant (Part I) (figure 6.20). They do not begin playing (another independent activity) any sooner (figure 6.19), or reduce their role in proximity maintenance any earlier (figure 6.23). Though Part II infants do make significantly fewer attempts to

get on to caregivers than Part I infants at 6 weeks, the gradual decline with age in attempts to get on caregivers after this age is no different in Part II than Part I infants (figure 6.27).

This indicates that independence in infant marmosets is not simply a product of a gradual decrease in care from caregivers. The growth of independence is more likely to involve changes in both the caregivers' and infants' behaviours, and to develop from the interaction of the two. This was also found by Ingram (1977). Other studies have argued that infants are mainly responsible for the development of independence (e.g. Kaufman, 1974, and Rosenblum, 1971 for macaques), but most are open to various interpretations (Suomi, 1976). In the present study, though time on caregivers is mainly controlled by the caregivers, the increase in play and other activities occurs on the initiation of the infants (see section 4.5a)) and thus independence would appear to progress by the joint efforts of infants and caregivers.

6.4) HOW LONG DO THE EFFECTS OF REDUCED LEVELS OF CARE ON THE INFANT LAST?

The time course of the effects of reducing care from fathers at 4 to 6 weeks and social interactions with siblings at 14 weeks on the behaviour of infants up to 22 weeks old can be followed by examining the figures given previously in this chapter which compare the behaviour of infants from Part II with those from Part I.

Of the behaviours which show significant differences between the two groups of infants, none do so after 14 weeks of age. The amount of time infants spend huddling shows no significant differences between Part I and Part II after 4 weeks (figure 6.24). The total time infants spend playing (figure 6.19), time spent off (figure 6.20) and

the number of attempts infants make to get on to caregivers (figure 6.27) are not significantly different between Parts I and II from 10 weeks onwards. The time infants spend grooming caregivers does not differ between the two groups from 14 weeks (figure 6.26). The longest lasting differences concern approaching and leaving, but by 18 weeks there are no significant differences between Parts I and II in the total number of approaches to caregivers, the total number of leavings from caregivers, or the infants' role in the maintenance of proximity to caregivers (figures 6.21, 6.22 and 6.23).

It would appear therefore that the immediate effects of reducing care and interactions are short-lived and that infants of 18 weeks are indistinguishable from similar infants which experienced no reductions.

The possibility of longer term effects of reduced levels of care and social interactions on infants will be investigated in chapter 7.

6.5) IMPLICATIONS OF THE RESULTS OF THE DRUG TREATMENT ON THE CAREGIVING/ CARE-SEEKING HYPOTHESIS

The basic assumption of the hypothesis offered in section 4.9) is that the distribution of an infant marmoset's time and activities amongst its various caregivers at any given age is determined by the balance between the amount of care sought by the infant and the amounts of care offered by individual caregivers at that age. Differences in care sought and care offered between different groups should therefore go some way towards explaining differences in behaviour of the different groups.

The two groups of infants observed in this study, Part I

infants and Part II infants, were matched in terms of housing conditions, family composition and observation schedule, and showed comparable levels of all behaviours measured when at 2 weeks of age. The family groups in Part II were then manipulated by drug treatment such that fathers offered less care to infants (in terms of grooming, approaching and picking up) at 4 to 6 weeks and siblings provided less social interaction (fewer approaches, less time with, less play, more ignores) at 14 weeks (section 6.2)).

If the hypothesis is to prove useful, differences in behaviour of Part II infants from Part I infants after 2 weeks of age should be understandable in terms of these reductions in care and social interactions and their effects on the caregiving/care-seeking equilibrium. In several instances the hypothesis has stood up to the experimental manipulation and the predictions derived from it have been borne out. Infants whose caregivers are drugged do spend less time in non - care-seeking activities and there are some increases in care-seeking behaviour. Infants continue to seek care from caregivers in order of preference, and no compensation among caregivers is found. On the question of maximum levels of care there is insufficient data available, and, contrary to the prediction, independence does not proceed any faster in infants whose caregivers have been drugged. These findings are discussed in more detail below.

①
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The hypothesis predicted that if the total care given is reduced, the infant must increase its care-seeking to make up the deficit. This was to a certain extent found to occur. Non - care-seeking activities (play and off) became less important at 4 and 6 weeks and the infant tended to spend more time staying close to caregivers (by huddling at 4 weeks and maintaining proximity to a greater extent at 14 weeks).

However, many care-seeking behaviours were not increased. The amount of time in contact with caregivers and the total frequency of tantrums by infants did not differ significantly between Parts I and II. Part II infants made fewer attempts to get on to caregivers at 6 weeks, spent less time grooming caregivers at 6 and 10 weeks, and showed fewer approaches to caregivers at 6 and 14 weeks. This, together with the absence of play at 4 weeks and reduced amount at 6 weeks, indicates that in general the frequency and variety of behaviours of Part II infants are reduced as compared to Part I infants. It is interesting that a reduction in care given should be associated with an apparent reduced variety of infant behaviours, particularly when considered in the light of the various separation experiments that have been performed on infant monkeys (e.g. Hinde & Davies, 1972, and Spencer-Booth & Hinde, 1971 on Macaca mulatta; Kaufman & Rosenblum, 1967 on M. nemestrina; Schlottmann & Seay, 1972 on M. fascicularis; review by Mineka & Suomi, 1978). In these experiments, infants have been separated from their mothers for periods of several days, sometimes by removal of the infant from the group, sometimes by removal of the mother. In all cases they experience a large decrease in, if not total disappearance of, care given. Under these conditions the infants of these species develop, after an initial period of agitation, a 'separation-induced depression' syndrome. This involves the infant sitting hunched over, rarely moving, any movements which do occur being very slow, rarely responding to social invitations or making social gestures, showing almost no play, appearing uninterested in its environment, but increasing its self-directed behaviour (Kaufman & Rosenblum, 1967; Kraemer et al, 1981).

Although the care reduction in the present study was much less severe than in the separation experiments, the Part II infants

nevertheless showed some of the symptoms of separation depression, i.e. reduction in locomotion and active social interactions.

One question relating to the hypothesis and posed in section 4.9) was how does an infant total up the amount of care it perceives itself to have received? That is, does it simply require a fixed total amount of care, regardless of which caregiver provides it, or are different family members rated differently according to the care they provide? Data on the care-seeking behaviour of Part II infants showed that infants have quite distinct preferences. Infants generally make more attempts to get on to siblings and fathers than twins, and mothers than fathers. Infants spend relatively little time grooming caregivers but tend to groom mothers more than any other. Most approaching and leaving is directed towards siblings and twins (table 6.1 and figures 6.35 to 6.38).

A comparison of Part I and Part II infants showed that their order of preference of caregivers for two behaviours (the frequency of attempts to get on caregivers at 6 weeks, and the frequency of approaches to caregivers at 14 weeks) did not change despite changes in the Part II caregivers' behaviour resulting from the drug treatment.

Infants would appear therefore to require care from particular individuals rather than simply a total amount of care. Caregivers cannot however be ranked in order of the infant's preference in any simple way since the different measures of care-seeking do not show the same order of preference. Presumably different caregivers can provide for different requirements (see Baskett & Johnson, 1982) and will be rated by the infants (i.e. preferred) according to which need is most important at any one time, and not in any simple linear hierarchy.

The drug manipulation study has therefore shown that in this

instance the notion of a straight balance between care-seeking and caregiving is too simple. The elements of care-seeking are varied and complex and will change as the immediate requirements of the infant change.

No differences were found between Part I and Part II in the relative proportions of care given by different caregivers (excluding the drugged caregivers) to the infant, even though care given had been reduced in specific caregivers in Part II, nor did any Part II caregiver give absolutely more care than in Part I. This indicates that the remaining (undrugged) caregivers in Part II were not compensating for the deficiencies in the drugged animals' behaviour. This is in line with the hypothesis since compensation would be expected where the total care available is increased (relative to that required) not decreased as in Part II. No competition for access to infants was observed either.

Ingram (1975a, 1977 & 1978) reported compensation in her captive groups of common marmosets in that the amount of carrying by fathers and mothers was sometimes inversely correlated. This was not found in either Part of the present study. However Ingram's family groups varied in size, the largest being of ten individuals, and this would affect the likelihood of compensation occurring. The family groups used in the present study (six members) are possibly smaller than some of those occurring under natural conditions (up to about ten members, Bucher, 1980 & pers. com.; Hubrecht, pers. com.; Stevenson, 1978b) therefore if compensation occurs in the wild it would not necessarily be expected to occur under these particular conditions of captivity since the total amount of care available to infants (i.e. the number of caregivers) is smaller and therefore less likely to exceed the requirements of the infant.

In future studies it will be important to observe larger groups of marmosets where competition could be expected to occur, and to carry out more detailed fieldwork on larger groups of animals. If compensation is found to occur in larger groups this will lend support to the suggestion that caregivers have particular levels of care which they are most likely to give to infants of particular ages ('normal maximum' levels) and will be evidence in favour of the caregiving/care-seeking hypothesis. The fact that caregivers in this study do not compensate is in agreement with the suggestion of the existence of these 'normal maximum' levels of care, as is the greater amount of time Part II infants spend in family huddles at 4 weeks (section 6.3d)).

In chapter 4 it was suggested that compensation in caregiving behaviours would be a useful insurance policy against short term deficiencies in another individual's caregiving abilities. Since compensation was not found to occur in Part II, it may be that this sort of compensation does not in fact normally occur. In situations where there are multiple caregivers, even if one is prevented from giving care, the loss is unlikely to be critical. Infants will probably still receive sufficient care to survive (unless it is the mother that is unable to give care while the infants are still dependent on milk).

Alternatively, the scale of reduction of care in Part II may have been insufficient to trigger any short term compensatory behaviour. This is feasible since the infants themselves do not respond very dramatically to the reduced care from fathers and siblings. They do not reduce their care-seeking from fathers and siblings very much (section 6.3b i)) or change their preferences for them (section 6.3b ii)). It would be interesting to experiment with more critical reductions in care, perhaps involving the mother, to test whether or not compensation could be induced.

One very noticeable aspect of the behaviour of Part II infants which was completely absent in Part I, was the attempts by infants to get on to their twins from 4 to 10 weeks of age. In some cases this resulted in the twins actually carrying infants for a short time. The appearance of this behaviour in Part II is likely to be related to the lack of compensation by mothers and siblings for the fathers' reduced level of care at 4 to 6 weeks. It is also relevant that much of the approaching and leaving by infants was directed towards twins (figures 6.37 and 6.38).

A possible explanation is that in situations where an important caregiver (in this case the father) fails to show as much care as expected, the infant can transfer some of its care-seeking behaviour to its twin. This is likely to be the most satisfactory solution to the infant (in terms of gaining more time with caregivers) at least in the short term, since the other caregivers (mother and siblings) will not compensate, whereas the twin is also experiencing the reduction in care and will also be seeking extra attention. A similar finding in Part I of the study (see section 4.5)) was that infants with more rejecting parents tended to spend more time with their twins than infants with less rejecting parents.

Transfer of attention has previously been reported in langurs (Presbytis entellus). When mothers were removed from the troop their infants sought care from and became attached to other adult females which then acted as principal caregivers, the infants' distress being alleviated by the availability rather than the adequacy of the caregivers (Dolhinow, 1978 & 1980). Similar behaviour has been seen to occur in bonnet macaques, Macaca radiata (Rosenblum & Kaufman, 1968). From the frequency with which transfers occurred in the langur study McKenna suggested that it may be possible for infants to change attachment objects

(i.e. caregivers) frequently without social injury (McKenna, 1979).

This is perhaps even more likely in the case of marmoset infants which are accustomed to several caregivers from birth, as opposed to langurs which are cared for principally by the mother, with the assistance of other females.

The results from Part II therefore by and large support the caregiving/care-seeking hypothesis, though modifications are required to take into account additional factors which can influence caregiving and care-seeking levels over and above the 'normal maximum' rates proposed to vary according to the age of the infant. This is discussed further in chapter 8.

CHAPTER 7 - Long Term Effects Of Altered Infant-Caregiver Relationships

7.1) INTRODUCTION

It has frequently been demonstrated that early experience affects the later behaviour of animals. Studies of mother-infant interaction in humans suggest that very early interaction patterns may be responsible for later interactional patterns as well as for the behavioural characteristics that develop in the child (Thoman, 1975). On a less subtle level, it has been shown that disorders of conduct, personality, language, cognition and physical growth in children can all be associated with the occurrence of maternal deprivation of some sort in the children's early life (Rutter, 1972 & 1979).

Non-human primates show similar sensitivity to their early social environment. For example, when mothers of 20 to 32 week old rhesus monkey infants were removed from them for six days, the effects of separation were still apparent 24 months later. The separated infants spent less time away from mothers, played a greater role in maintaining proximity to mothers, and were less likely to approach novel or mildly frightening situations than were non-separated controls (Spencer-Booth & Hinde, 1971). Under natural conditions also, differences in social development and social relationships in infancy and adolescence can lead to, for example, different reproductive tactics in adult life (e.g. gorillas, Harcourt & Stewart, 1981). In rhesus monkeys the type of rearing conditions (large or small social groups, presence or absence of infants) can also affect later interactions with infants (Holman & Goy, 1981).

It might therefore be expected that infants from Part I of this study and infants from Part II would show some evidence of their

different social backgrounds (i.e. level of care received) in their behaviour later on in life. Since caregiving behaviour is of central interest to this study, the long term effects of differences in care received by infant marmosets will be examined by investigating the quality and quantity of caregiving behaviour the infant subjects themselves, together with their twins, offer to the infants of the next set of offspring born into their families (i.e. their younger siblings) in relation to the type of caregiving relationships they (the subjects and twins) experienced as infants, i.e. undisturbed or drug-modified. Ideally this line of enquiry could be pursued further, the care subjects received as infants being compared with the care they give to their own infants. This was not possible in the present study since infant subjects were not kept to form new family groups when mature.

As a result of the procedure of using an infant from each successive set of offspring as a subject (see chapter 2) many infant subjects, together with their twins, were observed when they were older siblings to succeeding subjects. In Part I all subjects were observed both as infants and as older siblings, but subject numbers 7, 8 and 9 were siblings to Part II infants and were therefore not acting as caregivers under comparable conditions to the other Part I subjects. Data from Part I subject numbers 1, 2, 3, 4, 5 and 6 only therefore will be used in this chapter, together with the data from their twins which also became older siblings and were observed as such. In Part II, subject number 2, 3, 5 and 6 were watched both as infants and as older siblings in comparable conditions (i.e. both involved drug administration, see chapter 2) and data will be taken from these together with that from their twins.

7.2) DOES DRUG-INDUCED REDUCTION OF CARE EARLY IN LIFE HAVE LONG TERM CONSEQUENCES ON LATER CAREGIVING BEHAVIOUR?

To answer the question of whether or not drug-induced reduction of care to infants affects their behaviour later on when acting as caregivers, twelve animals from Part I will be compared with eight animals from Part II (see above) with respect to their behaviour towards the infants to whom they are older siblings. Since only one infant from each set of offspring was observed in any family, the caregiving behaviour of infant subjects and their twins is recorded towards one younger sibling in each case.

The subjects whose behaviour as older sibling caregivers is being examined will be referred to in the rest of this chapter as caregiving-infants to distinguish them from the other caregivers, older siblings discussed in previous chapters, and the infants to whom they are giving care. The infants to whom the caregiving-infants are giving care will be referred to as younger siblings.

Results from Part I and Part II caregiving-infants are compared using two-tailed Mann-Whitney U tests with a 5% significance level (Siegel, 1956).

a) Comparison of Part I versus Part II caregiving-infants

Comparisons between Part I and Part II caregiving-infants are made when the younger siblings are 2 weeks old only since after this time the caregiving-infants' behaviour in Part II may be affected by the drugging of the fathers in their family groups occurring when the younger siblings are 4 weeks old, and of course by their own experience of the drug when the younger siblings are 14 weeks. Thus, after 2 weeks, Part II caregiving-infants may behave differently from

Part I caregiving infants for reasons other than their own experience of reduced care when as infants.

The following behaviours will be compared: Time caregiving-infants spend with younger siblings, time spent carrying younger siblings, time spent grooming younger siblings, responsibility for initiation and termination of bouts of carrying of younger siblings, approaching and leaving between caregiving-infants and younger siblings, and tantrums given by younger siblings while with the caregiving-infants. Other behaviours, including contact, play, rejections, aggression and ignores are not examined since they virtually never occur between siblings and 2 week old infants.

Figures 7.1 to 7.3 show that Part I caregiving-infants spend rather more time with 2 week old younger siblings than do Part II caregiving-infants, and also more time carrying them and grooming them, but the differences between them are not significant.

Figure 7.4 shows the mean frequencies of initiation and termination of bouts of time carrying younger siblings by caregiving-infants and younger siblings in Parts I and II. There are no significant differences between the number of times Part I and Part II caregiving-infants pick up younger siblings, or rub-off younger siblings, or in the number of times younger siblings get on or off Part I versus Part II caregiving-infants. However, in Part II the caregiving-infants are responsible for significantly more of the initiations and terminations of bouts of time carrying than are the younger siblings, while in Part I there are no significant differences between caregiving-infants and younger siblings in either the frequency of initiations or of terminations of bouts of time carrying.

Figure 7.5 shows the mean frequencies of approaching and leaving between caregiving-infants and younger siblings in Parts I and

Figure 7.1

Mean percentage of time caregiving-infants spend with younger siblings in each Part of the study. Vertical lines indicate standard errors. Open bar denotes Part I caregiving-infants, hatched bar denotes Part II. NS indicates nonsignificant difference between Part I and II results (two-tailed Mann-Whitney U test).

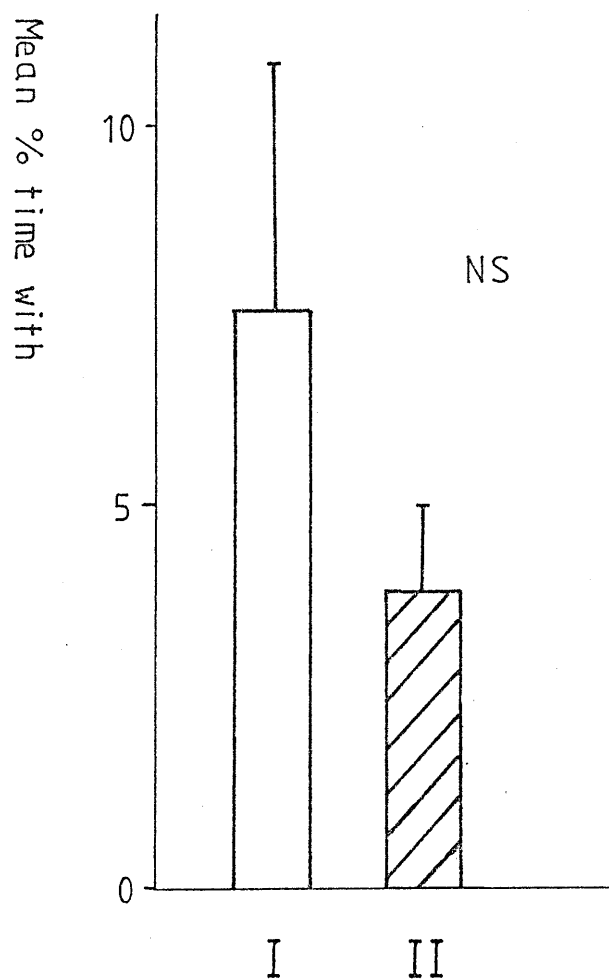


Figure 7.2

Mean percentage of time caregiving-infants spend carrying younger siblings in each Part of the study. Vertical lines indicate standard errors. Open bar denotes Part I caregiving-infants, hatched bar denotes Part II. NS indicates nonsignificant difference between Part I and II results (two-tailed Mann-Whitney U test).

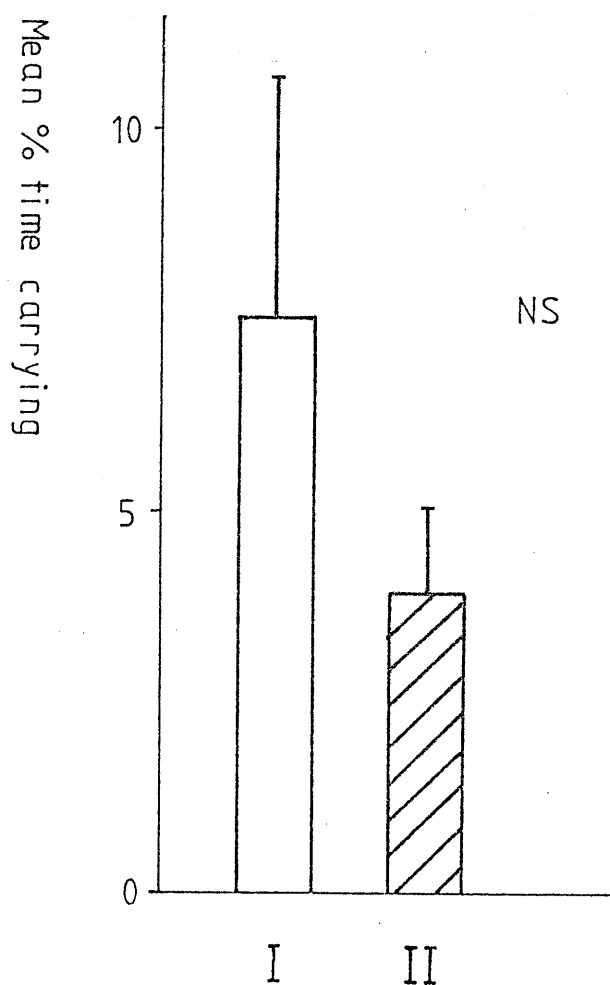


Figure 7.3

Mean percentage of time caregiving-infants spend grooming younger siblings in each Part of the study. Vertical lines indicate standard errors. Open bar denotes Part I caregiving-infants, hatched bar denotes Part II. NS indicates nonsignificant difference between Part I and II results (two-tailed Mann-Whitney U test).

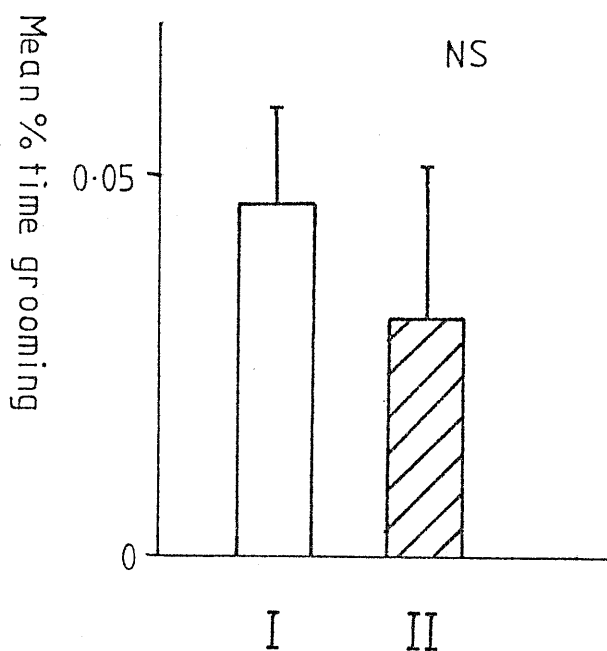


Figure 7.4

Mean frequencies of bouts of time carrying by caregiving-infants that are initiated and terminated by caregiving-infants and by younger siblings in each Part of the study. 'On' denotes the initiation of bouts of carrying. 'Off' denotes the termination of these bouts.

Hatched bars denote 'ons' and 'offs' by caregiving-infants. Open bars denote 'ons' and 'offs' by younger siblings. Vertical lines denote standard errors. Symbols show results of two-tailed Mann-Whitney U tests for comparisons between data indicated by arrows.

* $p < 0.05$. ** $p < 0.02$. *** $p < 0.002$. NS nonsignificant.

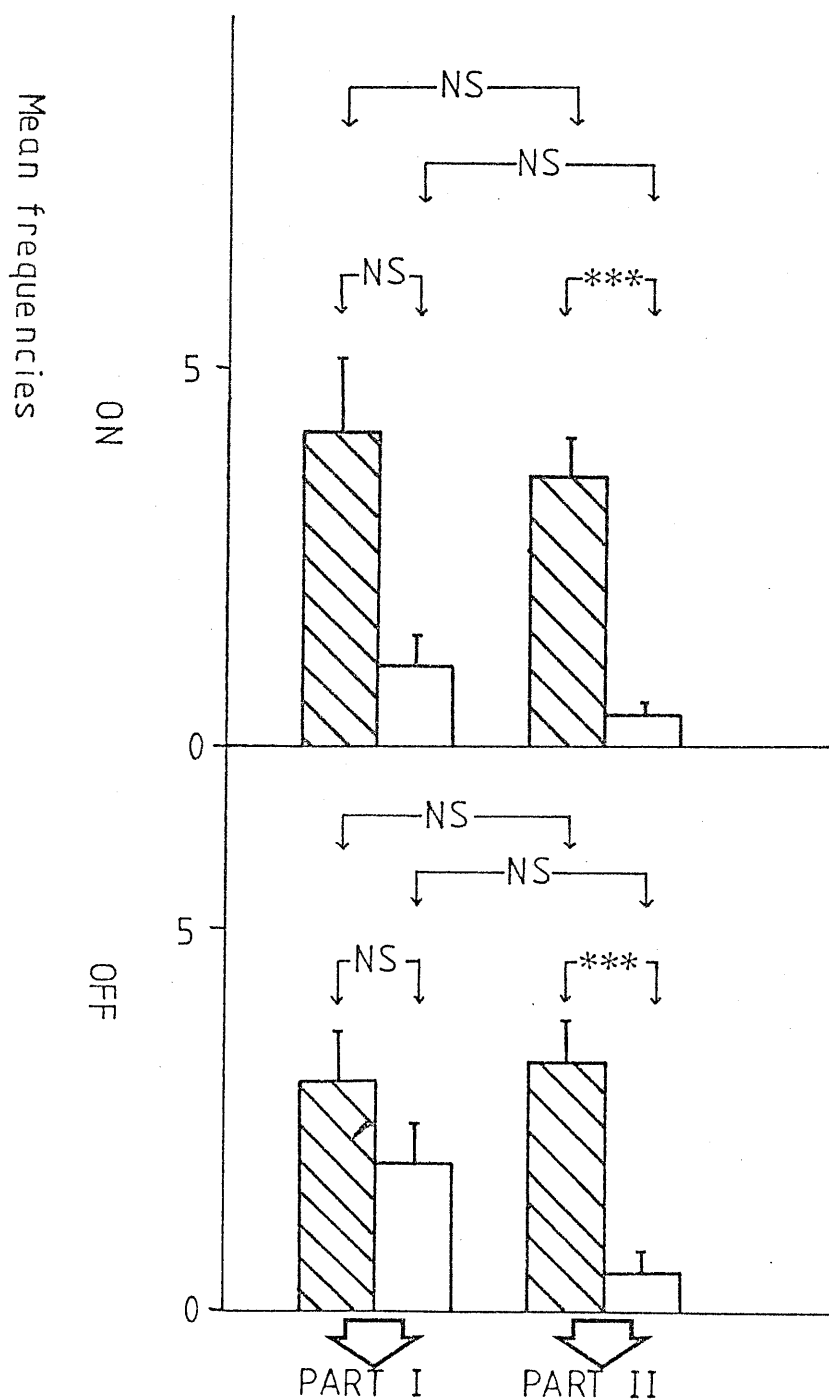


Figure 7.5

Mean frequencies of approaching and leaving between caregiving-infants and younger siblings in each Part of the study.

Hatched bars denote approaches and leavings by caregiving-infants. Open bars denote approaches and leavings by younger siblings.

Other conventions as in figure 7.4.

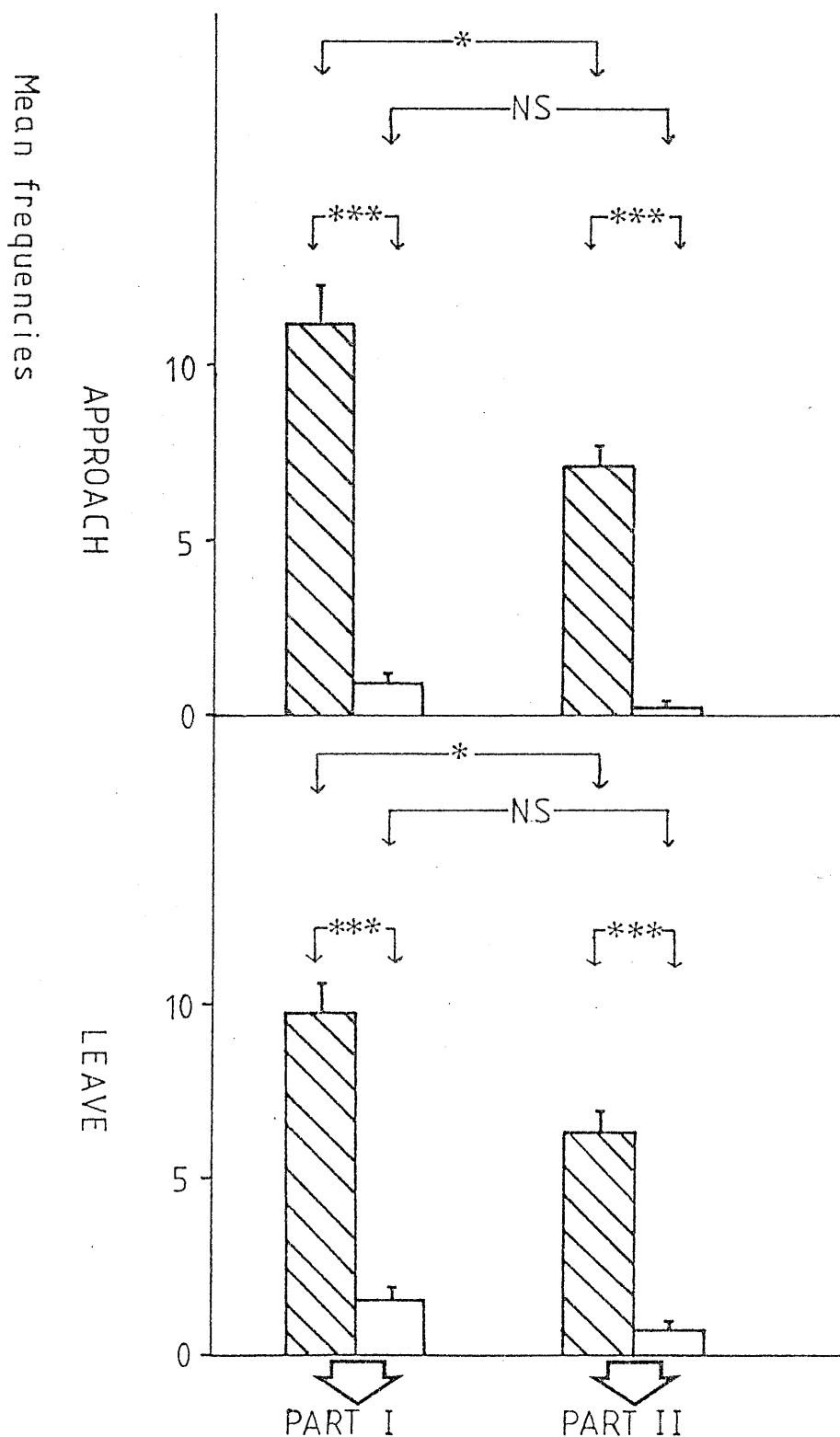
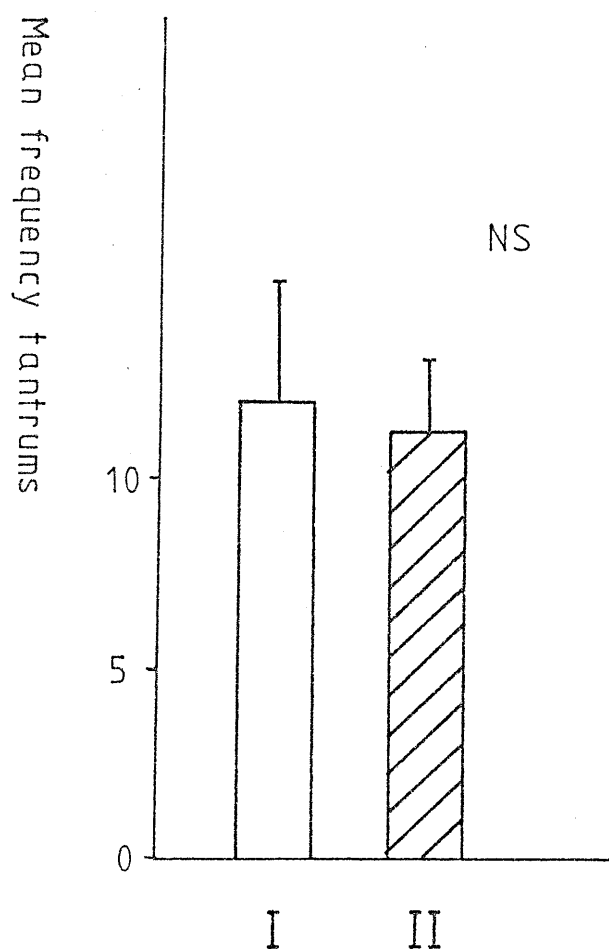


Figure 7.6

Mean frequency of tantrums given by younger siblings while with caregiving-infants in each Part of the study. Vertical lines indicate standard errors. Open bar denotes Part I results, hatched bar denotes Part II. NS indicates nonsignificant difference between Part I and II results (two-tailed Mann-Whitney U test).



II. Caregiving-infants both approach and leave younger siblings significantly more often than younger siblings approach and leave caregiving-infants in both Parts of the study. There are no significant differences between the number of times younger siblings approach or leave caregiving-infants in Part I versus Part II, however Part II caregiving-infants both approach and leave younger siblings significantly less often than do Part I caregiving-infants.

The frequencies of approaches, leavings, initiations and terminations of bouts of time carrying are insufficiently large for responsibility indices such as %AP.I - %LV.I to be calculated.

Figure 7.6 shows that there is no significant difference between the number of times younger siblings display tantrums with Part I and Part II caregiving-infants.

b) Conclusions

The results given in section a) above reveal little or no difference in the behaviour of Part I and Part II caregiving-infants, the only significant differences being that infants which experienced reduced care themselves approach and leave younger siblings less often than infants which received undisturbed levels of care.

There are three possible explanations for this apparent lack of long term effects of drug-induced reduction of care to infants. The first is simply that the reduction in care was not sufficiently large to have any noticeable effects. This has been suggested already (section 6.5) as a possible reason for the lack of difference in number of tantrums given by Part I and Part II infants. If care had been reduced more severely, the differences in time with, carrying and grooming of younger siblings (figures 7.1 to 7.3) between Part I and Part II caregiving-infants may have become significant and long term effects of reduced care more apparent.

The second explanation is that the particular elements of care which were reduced (the number of times fathers pick up infants, the time fathers groom infants, the time siblings spend with infants, and the frequencies of approaching and leaving by fathers and siblings to and from infants) were not ones which would affect later caregiving behaviour. Ruppenthal et al (1976), in discussing "motherless mother" rhesus monkeys, state that physical contact either with peers or with their own infants immediately after birth greatly reduces the probability that motherless mothers would be inadequate and abusive maternally. In the present study contact and huddling were not reduced but tended rather to increase in Part II over Part I infants (figures 6.24 and 6.25). It is therefore possible that the infant marmosets in Part II received sufficient physical contact to offset the reduction in other aspects of care and consequently did not behave inadequately as caregivers when compared with Part I.

The third explanation is that marmosets may be highly adaptable and be capable of recovering from any early social deficits rapidly enough for the deficits not to affect their behaviour several weeks later. Chapter 6 showed that changes in infants' behaviour following drugging of their caregivers at 4 and 14 weeks had disappeared by 18 weeks. Caregiving behaviour shown by infants to younger siblings at about 25 weeks of age may therefore be simply too far removed from the experience to be affected by it.

The data therefore show very few real long term effects of drug-altered infant-caregiver relationships on the infants' later caregiving behaviour towards 2 week old younger siblings, but do give indications that it could be affected under more severe conditions of care reduction.

CHAPTER 8 - Concluding Comments

This study of infant-caregiver relationships in captive common marmosets has largely fulfilled the aims set out in chapter 1: A detailed quantitative account of the social development of infants has been produced, extending previous work in this area. A small number of underlying factors have been suggested to control infant social behaviour and a simple hypothesis based on these constructed to try to explain some of the changes and differences observed between infants from different groups and of different ages. This hypothesis has been investigated by experimentally manipulating the behaviour of caregivers and found to be useful though not wholly adequate. These points are discussed in more detail below.

The results from the first Part of this study have established the course of development of marmoset infant-caregiver relationships during the first 22 weeks of life under undisturbed captive conditions, and can be summarized as follows:

Between the ages of 2 and 6 weeks the time infants spend with all family members decreases sharply, though the decline is less dramatic for mothers and twins than for fathers and siblings. Time on all caregivers declines to zero, while time in contact with mothers and twins increases. The amount of time infants spend playing with twins also increases at this time. As contact with mothers and twins later decreases, play with siblings increases.

The decrease in the amount of time infants spend on caregivers is primarily due to changes in the behaviour of caregivers rather than of infants. Caregivers pick up infants progressively less often from 2 to 6 weeks and increase their relative frequency of rejections. When rejected by a parent, the infant tends to spend its time with its

twin.

The increase in time in contact with the mother occurs on the initiation of the infant. As might be expected (since twins are also infants) both infant and twin contribute to the increase in play between them, whereas the increase in play with siblings is mainly due to the infant.

Siblings are relatively unimportant as carriers of infants but become prominent later on as play partners. Twins are important at all ages, first for contact and later for play, and appear to act as close companions in situations when the parents are no longer readily available (i.e. no longer willing to carry infants for long periods), and before the infants are old enough to take on playful interactions with the siblings.

The age of 10 weeks seems to mark a change in the responsiveness of caregivers towards infants and has been called a period of 'baby transition'.

Parents and siblings do not generally compensate for differences in each others' behaviour towards infants, however twins appear to compensate by spending more time with infants which have rejecting parents (probably because the twins too experience the rejections of the parents).

Data concerning the behavioural consequences of rejections and rub-offs by caregivers suggest that infants do not rate caregivers equally and that caregivers have a limit to the amount of time they are prepared to devote to infants: An infant which has been rubbed off does not attempt to interact again with that caregiver but is more likely to try another caregiver. An infant which has been rejected however, is likely to interact again with that caregiver, indicating that it is attempting to get on to a particular caregiver, and not just

to get on.

These results show that the quality of the infant's relationships with each kind of caregiver changes with age and that different kinds of caregivers come to have different relationships with the infant. This is in general agreement with other work carried out on captive Callitrichids (e.g. Box, 1975a, 1975b, 1977; Epple, 1975; Ingram, 1975a, 1977; Kingston, 1969; Snyder, 1974; Vogt, 1978).

From an examination of the results summarized above a simple hypothesis, based on two underlying behavioural parameters, was proposed in an attempt to explain the distribution of an infant's time and activities amongst its various caregivers. The two parameters are the tendency of an infant at a given age to seek a certain level of care, and the tendencies of family members to offer a certain level of care. This caregiving/care-seeking hypothesis suggests that differences in the amount of care individuals are prepared to give, and in the amount infants seek, and the different ways these varying levels are combined in family groups could account for observed differences in infant-caregiver relationships between different groups of animals. For example, if an infant perceives that the amount of care it has received is less than the amount it seeks and if this is more than the caregivers will offer, it would be expected that the infant would continue to seek care, that it would be rejected, and that caregivers would show no competition over which individual cared for the infant and no compensation. However, if the amount of care offered by caregivers greatly exceeded the amount sought by the infant, it would be expected for caregivers to compete for access to infants and that highly caring individuals would compensate for low amounts of care offered by less caring members of the group. The hypothesis is discussed more fully in section 4.9).

Predictions were drawn from this hypothesis which were investigated in Part II of the study using a neuroleptic drug to modify amounts of care offered by caregivers. Several predictions of the caregiving/care-seeking hypothesis were borne out by the results of Part II of the study while some were not. These results are summarized below.

As predicted, infants do spend less time in non - care-seeking activities when fathers are drugged at 4 weeks, but this is not the case when siblings are drugged at 14 weeks. Contrary to the predictions, infants do not expend a great deal of effort (i.e. time and activity) in extra care-seeking. Rather they seem to reduce the frequency and variety of their behaviours. Infants approach (i.e. seek care from) fathers less at 6 and 10 weeks when fathers have been drugged at 4 weeks, but drugging siblings at 14 weeks does not have this effect. In general infants do not significantly reduce their care-seeking from drugged animals, though a reduction had been predicted. Infants continue to seek care (attempt to get on, approach) from caregivers in order of preference despite changes in the caregiving behaviour of fathers and siblings which have been drugged. This had been predicted, though a drop in the preference for the animals which had been drugged had also been expected. No compensation was found by any caregiver for any caregiving behaviour measure, as predicted, and no competition for access to infants was observed. The data were inconclusive on the question of whether or not animals were giving care at their 'normal maximum' level, further experimentation and fieldwork are required to answer this question. Finally, contrary to the prediction, independence did not proceed any faster in infants whose caregivers had been drugged.

In cases where the model was not sufficient to explain the observed behaviour, it has provided further insight into the complexity

of infant development and indicated how the study could be improved upon. The main problem would appear to be that though the level of caregiving in the drugged animals was reduced significantly with respect to several behaviours, the overall decrease caused by the drug treatment was not dramatic. This resulted in little reduction in care-seeking from drugged caregivers, and very little extra care-seeking from other caregivers. In addition, there were very few long term effects on the infants' later caregiving behaviour towards 2 week old younger siblings, though the data did indicate that greater effect might be produced under more severe conditions of care reduction (see chapter 7).

The drugging of siblings had less effect on the infants' behaviour than did the drugging of fathers. This may be because social interactions with siblings are relatively less important to the infant than care from fathers, but is perhaps more likely to be due to the age difference of the infants when fathers and siblings were drugged. 14 week old infants are far more independent than 4 week old infants. In addition, by the time the siblings were drugged the infants had already experienced drugged fathers. It is possible that the infants habituate to small changes in care received, and having adapted to the drugging of the fathers, did not respond to the drugging of siblings. Had many more families and infants been available for observation, a better experimental schedule would have been to drug only one category of caregiver for each individual infant, to drug the various different caregivers at the same infant age, and to repeat for several different ages.

As described in chapter 6, the rating of individual caregivers by infants appears to be more complex than originally implied in chapter 4, since it varies with which behaviour is concerned and

presumably with the time elapsed since it was last performed. Similarly, the control of infant independence consists of more than simply a reduction in levels of care given by caregivers over time. Until relatively recently many studies have neglected the effects of the infant on the caregiver's behaviour (see discussion in Rutter, 1979, also Hinde, 1979), but the development of infant independence does, in this study, seem to be influenced by both caregivers' and infants' behaviour.

If 'care' is defined in terms of investment (see section 6.1)), then the particular level of care given by a caregiver should depend on the balance between the costs and benefits of caring to the caregiver. The performance of caregiving behaviours with a relatively higher cost, that is those which take more effort by the caregiver e.g. carrying infants, could be expected to be more closely maintained at the optimal (i.e. 'normal maximum', see section 4.9)) level than those behaviours which take little or no apparent effort on the part of the caregiver, e.g. sitting in contact with an infant. Carrying could therefore be expected to conform to the caregiving/care-seeking hypothesis more closely than, for example, contact. It is however difficult to evaluate this possibility with the present data since there is little overlap in infant development between time on and time in contact with specific caregivers. For example, as time on mothers decreases so time in contact with mothers increases (figures 4.2 and 4.6). It would be useful in further studies designed to test the caregiving/care-seeking hypothesis to concentrate on aspects of care which take most effort such as carrying and to watch infants at more frequent intervals early in life when these behaviours are most prominent.

It is also important to determine more specifically what the 'cost' of caregiving actually is. Although all caregiving behaviours must take some time and energy to perform, is there in fact much cost

(over and above the normal maintenance level of energy expenditure) attached to behaviours such as contact, huddling and grooming? Even carrying newborn infants does not prevent individuals from carrying out any of their other daily activities. This is in contrast to other primates in which the neonates need assistance from their caregivers in order to cling on to them (e.g. chimpanzees Pan troglodytes, Van Lawick-Goodall, 1967; gorillas Gorilla gorilla, Schaller, 1963), or cannot effectively cling at all and must be wholly supported (e.g. humans, Mason, 1968), or must be left in nests and periodically visited (various lemurs e.g. Microcebus, Cheirogaleus, Phaner and Varecia, Klopfer & Boskoff, 1979). Perhaps the relatively low cost of many caregiving activities has been an important factor in promoting the development of multiple caregiving in marmosets.

All caregiving activities imply some sort of survival benefit to the infant but benefits to the caregivers are usually assumed rather than defined. The most obvious advantage to caregivers is the genetic one of promoting the survival of their genes. This applies to parents and to other close relatives of the infant (i.e. siblings). Other benefits include practice in caring for infants (Epple, 1975; Lancaster, 1972), the development of tolerance towards infants (Holman & Goy, 1981) and the opportunity to remain for longer in the natal group. Group living is presumably safer than solitary living for young marmosets and it may be difficult for individuals to set up new territories of their own until they have had several years experience as adults (Neyman, 1980). Perhaps by assisting parents in raising infants, older offspring are allowed to stay in the group further beyond maturity than would be the case if they did not give care to infants.

Scollay and DeBold (1980) and Quiatt (1979) have suggested that for langurs (Presbytis entellus) allomothering (i.e. caregiving

by adult females other than the mother) is merely an extension of a general adaptation to provide adequate care for one's own infant, i.e. a general pattern of interest in infants, and may be fortuitous rather than selected for in its own right. In other words, allomothering may not have any adaptive benefit itself (to the caregivers) but rather may have been selected for as part of a "total behavioural complex" (Scolly & DeBold, 1980). This is less of a possibility in the case of marmosets since in Callitrichid groups, the caregivers are likely to be more closely related to the infant and to each other than in langur groups, and though there is variability between individuals in the amount of care given (Box, 1977) in general all group members are seen to give care whereas this is not necessarily the case with langurs (Dolhinow, 1980).

It seems likely that care given to infants by siblings differs in function from care given by parents. In the case of parents, the returns to the caregiver for the effort expended in caring are probably almost entirely in the form of reproductive success, i.e. the successful rearing of offspring. In the case of the father this includes the opportunity to remain in proximity to the mother while she comes into post-partum oestrus. This proximity results from the father's extensive care of the infants in their early weeks of life.

In contrast, siblings may gain in several ways described above. The somewhat anthropomorphic term 'care' is probably a less accurate description of interactions between siblings and infants than is a phrase such as 'investment of time' since siblings probably benefit as much from the activity as do infants.

The infants themselves probably obtain different sorts of benefit from care from siblings as opposed to parents, even when the individual caregiving behaviours involved are the same. This could

result from differences in the quality, quantity or patterning of the caregiving behaviours. An example of this has been observed in human children which interact more, and use more 'positive' behaviours, with parents than siblings and are suggested to gain different aspects of socialization from each kind of caregiver. 'Positive' behaviours were defined to include compliance to commands, laughter, talk and touching, as opposed to 'negative' behaviours such as threats, crying, non-compliance to commands and tantrums. In their relations with parents, the children were suggested to learn appropriate ways to elicit positive responses from others, especially from individuals more powerful than themselves. With siblings, they were said to learn how, when, and with whom to use aversive control techniques and how to respond to coercion from others (Baskett & Johnson, 1982).

As suggested previously, the differences in care from parents and siblings could be further investigated by manipulating care from these different types of caregiver when infants are of equivalent ages, rather than as here, when infants were of different ages.

Further research into the caregiving/care-seeking hypothesis should therefore concentrate on aspects of care which can be easily defined and measured, and whose costs to the caregivers and benefits to the caregivers and infant can also be determined.

The use of different group sizes would allow the total amount of care available to the infant to be varied, assuming differences in the age and experience of individual caregivers, the age structure of the group and the physical condition of the individuals could be controlled for. However, complications could arise when making comparisons between infant-caregiver relationships in groups of different sizes since the social nexus of all individuals would change with changes in group size and this could be reflected in the infant-

caregiver relationships present. For example, Ingram (1975a) found that mothers in small family groups (containing one or two sets of offspring) fed and carried their infants for smaller amounts of time than did mothers in larger family groups (three or four sets of offspring).

An alternative line of enquiry would be to vary the costs of giving care. For example, if animals have to forage for long periods in order to obtain sufficient food, the time spent caring for infants becomes more costly to the extent that it interferes with foraging. This could be investigated experimentally under captive conditions by, for example, only supplying food when individuals are not carrying infants, or making food gathering a time-consuming manipulative task (e.g. Baldwin & Baldwin, 1976).

Using these methods the hypothesis could be expanded to take account of changes in the caregiving/care-seeking balance brought about by factors independent of the infants which are seeking the care.

This has been the first study which has used drug-modification of behaviour to test a social developmental hypothesis and it is possible that if levels of care had been further reduced the predictions indicated in chapter 4 would have been more fully borne out. Part II infants' behaviour was already apparently back to normal by 18 weeks (section 6.4)), and the lack of difference in frequencies of tantrums between Part I and Part II infants may indicate that care was not sufficiently reduced to cause the infant noticeable discomfort, or that the reduction was such that the infant could cope by reducing its requirements for care. Plasticity in requirements and short term changes in caregiving dependent upon immediately preceding events and the social context may well prove to be important factors which need to be taken into account in the hypothesis in addition to care-offering and

care-seeking at levels typical for infants of specific ages. Improvements in the environment and changes in the physical condition of caregivers and of infants will also affect the amount of care which is required and caregivers may respond by altering the levels they give. Carlisle (1982) has pointed out that parental care patterns vary within species and may often be adjusted by individuals according to prevailing or projected conditions. Further complexities may have been added in this study by the fact that the effects of the drug-induced changes in behaviour on the infant may be indirect as well as direct, that is, mediated through their effects on other individuals in the group. This is virtually impossible to control for in studying a species living in small social groups with multiple caregivers and therefore close relationships between all group members.

In conclusion, the suggestion of a balance between care offered and care sought is in general a useful point from which to begin a study of caregiving relationships but it is too simplistic to account for all differences between groups. For a more complete understanding of infant social development other factors (as mentioned above) independent of infant age and those which may promote short term changes in levels of care given or required must also be taken into account. In general terms however, the caregiving/care-seeking hypothesis can be used to describe and explain the course of infant social development in species with multiple caregivers.

APPENDIX 1

Behaviour check sheet for
preliminary drugs tests.

PRELIMINARY DRUGS TEST

Subject

Cagemate

Weight of subject

POST-DRUG ☐

Method of administration :

Social Interaction Marker Frequencies

TW = Cagemate (twin)

	TOTAL
DM app. TW	
DM lvs. TW	
TW app. DM	
TW lvs. DM	
DM grooms TW	
TW grooms DM	
DM initiates playbout	
- successfully	
- unsuccessfully	
TW initiates playbout	
- successfully	
- unsuccessfully	
DM ignores TW	
DM/TW contact	

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